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THE UNIVERSITY OF ALBERTA

Schedule-Induced Polydipsia: Attenuating Effects With Decreasing Food Granulation Size

by

David Gerald Mumby

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Department of Psychology

EDMONTON, ALBERTA

Fall, 1988

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Date.. December.. 30,.. 1987.

Abstract

A two-phase experiment examined the effects of food texture on the generation of schedule-induced polydipsia. In the first phase, the acquisition and final levels of drinking for two weeks of daily 50-minute sessions were observed in groups of rats that differed only in the granulation of the food that they received on a fixed-time 60-second schedule. Volume of water consumed by rats that received scheduled delivery of granulated food of particle sizes larger than 0.6mm was not different than that of a control group that received standard 45mg food pellets. As the particle size decreased below 0.6mm rats drank significantly less, and the degree of this attenuation was greater the smaller the particle size. In Phase 2 additional drinking measures were obtained, and a variety of other behaviours were observed, with drinking at asymptote, for animals trained with different granulation sizes. Attenuated polydipsia in rats receiving finer granulated food was due mainly to decreased duration of post-food drinking bouts. Time spent drinking declined over the course of a 50-minute session for rats receiving granulated food smaller than 0.8mm while it did not for those receiving coaser food or pellets. Decreases in time spent drinking were accompanied by increases in the facultative behaviours of rearing and grooming. The results are interpreted as supportive of a sensitization model of schedule-induced polydipsia.

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I. Introduction

Falk (1961a) was the first to report that hungry rats consume prodigious amounts of water while bar pressing for food on a variable-interval schedule. This phenomenon was subsequently termed "schedule-induced polydipsia" (SIP) to denote the excessiveness of the behaviour as well as its dependence on intermittent delivery of a reinforcer (see Section V for details concerning characteristics of SIP).

Several researchers have since added to the list of factors that influence the amount of water that rats imbibe in under conditions of intermittent food delivery. It is known that a response contingency is not necessary for the generation of the effect, that drinking varies directly with food deprivation level (Falk, 1971), and is a function of the amount of food per delivery (Millenson, 1975; Reid and Staddon, 1987). Other factors, such as the interfood-interval length (Falk, 1971), and the temporal availability of water within the interfood interval (Flory and O'Boyle, 1972) have also been noted to effect SIP. A number of pharmacological agents have been tested for their effects in the SIP paradigm (Wallace and Singer, 1976, provide a review). But regardless of the accumulation of facts about SIP an adequate explanation of the processes involved in the generation and maintenance of this peculiar phenomenon remains elusive. Many attempts have been made invoking either physiological or behavioural explanations, but none have been able to account for all of the data

(Staddon, 1977, and Wetherington, 1982, provide good reviews; see Section V for details on factors influencing SIP, and a review of theoretical explanations of SIP).

The most common procedure for producing SIP is to deliver on an intermittent schedule single food pellets to hungry rats with free access to water. Recently, the surprising observation was made that the development of SIP is attenuated in rats who receive 45mg of dry food powder instead of the standard 45mg pellet on an intermittent schedule. (Beck, Huh, Mumby, and Fundytus, 1988). Furthermore, rats already made polydipsic with the scheduled delivery of pellets quickly stop their excessive drinking when powder replaces pellets. These researchers proceeded to investigate some of the potentially relevant differences between the two forms of food for their role in determining the effect on SIP. The topography of the consumatory response (rats can pick up pellets to eat them while powder must be licked up) was one factor found to be unimportant. Since the food powder used in these experiments was made from ground pellets the effect could not be attributed to simple food constituent or flavour differences. Although there was found to be a reciprocal relation between drinking and the amount of food associated feeder behaviour, a causal link between these two behaviours was not ascertained. Finally, the most intuitively obvious difference that remained between pellets and powder was texture, or particle-size of the food. The finding that coarse

granulated food is just as effective as pellets in producing SIP, while finely powdered food is not, suggested that texture may be the critical factor in powder attenuated polydipsia (Beck, et al., 1988).

The purpose of the present study was to further elucidate the role of food texture in the generation of SIP. To this end, a two-phase experiment was conducted in which different groups of rats received scheduled delivery of granulated food differing in particle size. The coarse and fine granular foods used in the Beck et al., (1988) study were composed of a large range of particle sizes and, therefore, one of the objectives of the current experiment was to delineate more precisely the particle-size of food necessary to generate SIP, and also to provide enough levels of this independant variable to allow description of the relationship between particle-size and SIP.

In the first phase of the experiment the effects of food granulation size on the development of SIP over a number of sessions was observed. The hypotheses were that rats trained on finer granulation food would achieve lower levels of polydipsia, as measured by volume of water consumed, than would those trained on coarser food, and that rats trained with the finest of powdered food would not become polydipsic at all, as was found in the Beck, et al., (1988) study.

In the second phase of the experiment a number of additional behaviours were examined within the same

experimental conditions as in the first phase, and with rats performing at asymptotic levels of drinking. Since drinking is not the only behaviour engaged in during the interfood interval, it is possible that some other behaviours may vary in their prevelance as a function of food granulation size. There may be a systematic increase in a particular behaviour as drinking decreases as a result of decreasing food particle-size. Roper and Nieto (1979), for example, found that grooming in rats increases when levels of polydipsia are decreased by increasing body weight. Reid and Staddon (1982) found increased feeder activity to be associated with decreased drinking as a result of increasing reward magnitude.

It was felt that to follow the development of possible group differences in several behaviors over all sessions would yeild relatively superfluous information, as this has already been done in this lab for a number of treatment groups similar to those used in the present study, and those results are reported in Beck, et al. (1988). These researchers found that there were no significant differences in the prevelance of any behaviours on the first training session between rats receiving pellets or powdered food; no group differences on any behaviours were obtained until after a number of sessions.

Also, in the present experiment, the patterns of occurrence of behaviours within the interreinforcement interval and over a session were described. Such temporal

breakdown of total session values on a number of behaviours might yield data that better describes the nature of observed treatment effects than would single measures summed over an entire session (Staddon and Ayres, 1975; Roper and Nieto, 1979). Decrements in drinking measures produced by the treatments might be accompanied by failure of drinking to be entrained by food delivery (Reid and Staddon, 1987).

The single measures of total water intake, or time spent engaged in a particular behavior, would provide limited insight into how a difference in granulation size effects these responses. Differences in volume intake, or amount of time engaged in other behaviors, could be caused by differences in the number of bouts of these behaviors, in the duration of these bouts, or both. For example, Keehn and Stoyanov (1986) found that the development of polydipsia was characterized by an increase in the frequency of drinking bouts over sessions, while the duration of drinking bouts remained unchanged. Therefore, in the second phase of the experiment multiple measures of drinking and other behaviors were taken, including the percentage of time the rats spend in each behavior, the number of bouts of each behavior, and the duration of these bouts.

In sum, the hypotheses were that decreasing the food granulation size would produce similar decrements in SIP as measured by volume intake. Selective increases in a particular behaviour were not expected to result from this manipulation, as none were found in the apolydipsic rats

that received powdered food in the Beck et al. (1988) study. Because it was expected that excessive volume intake would be exhibited by those rats receiving the coarsest of granular foods, it was also expected that drinking in these rats would show other characteristics common to pellet induced polydipsia, namely entrainment by food delivery (occuring in temporal proximity to, and following food delivery). If drinking was found to be excessive and schedule induced in any group of rats, it was expected that the temporal distribution of other behaviours within the interfood interval for these animals would be similar to that for standard pellet polydipsia controls.

To obtain the expected results would seem to mitigate against all but one of the existing models of SIP: the sensitization model described by Wetherington and Riley (1986). The model holds that the excessive drinking of the polydipsic rat is the result of repeated presentation of a stimulus (food) which initially is only a weak stimulus for the elicitation of an unconditioned drinking response. The food stimulus becomes increasingly more potent as an unconditioned drink eliciting stimulus as its intermittent presentation continues. This is exactly analogous to behavioral sensitization with repeated amphetamine dosing (Robinson and Becker, 1986).

The previous findings of Beck et al. (1988) suggest that if the sensitization model approximates the true mechanisms involved in SIP, then some aspect of powdered

food scheduling prevents the process of sensitization of the drinking response. Sensitization theory predicts that behavior that is less sensitized in one animal than in another, whether due to differences in frequency of stimulus presentation or to stimulus intensity differences, will have a greater tendency to habituation within a series of repeated presentation of the eliciting stimulus (details of sensitization theory can be found in Section VI). Therefore, one additional hypothesis in the present study, which served as a test of the sensitization model of SIP, was that rats which drank less total volume during a scheduled delivery session would also tend to show greater declines in drinking over the course of that session.

II. Methods

A. Animals:

Subjects were 56 male Sprague-Dawley rats (University of Alberta, Ellerslie), approximately 7 weeks old, and weighing 215-250g at the beginning of the experiment. The rats were housed individually in animal quarters maintained at 22 C, 51% humidity, and on a 12:12 light-dark cycle with lights on at 0800. All subjects had ad lib access to water, but not food, in their home cages.

B. Apparatus:

Six identical test chambers, measuring 20cm x 23cm x 23cm, with opaque walls and transparent ceiling were used. The floors were covered with fresh wood chip litter at the beginning of each session, and the walls and ceiling were wiped thoroughly after each session. A water dipper delivered 45mg of granulated food from a trough, or a 45mg pellet, to a 0.8cm diameter hole in the floor of a feeder cup 3.4cm in diameter, located 7cm above the floor. Care was taken to ensure that all treatment groups would be receiving the same amount of food regardless of the granulation size, and that the amount delivered would be consistent over a session. Dipper cups for each food granulation size were individually machined and calibrated to deliver approximately 45mg of food in a reliable fashion. Tests for this reliability were conducted by weighing several sample

dipper-fulls of the various food preparations and machining the cups to approximate the desired 45mg capacity. A water spout protruded approximately 1cm into each chamber through a hole 7cm above the floor and 15cm to the left of the feeder cup. The spouts were attatched to the barrell of a graduated burette allowing measurement of water intake to the nearest 0.1ml. The testing room was dimly illuminated with red ambient light provided by overhead fluorescent lights covered with red Mylar film. An electric fan provided air circulation and background noise (65db SPL) within the testing room. Observation of the animal was permitted via a mirror mounted at a 45 degree angle above each chamber.

All six chambers were wired through an electronic relay system attatched to a digital timer, thereby allowing for their simultaneous operation. Therefore, the vibratory and auditory stimuli that accompanied the firing of the delivery mechanism was the same for all six chambers.

C. Procedures:

Phase 1.

Subjects were food-deprived to 80% of their pre-experimental free -feeding body weights and maintained at this weight throughout the study with daily rations of Purina laboratory rat chow. Fourteen days of adaptation to the restricted feeding regimen were allowed for all subjects before training commenced. Experimental sessions and

weighing took place between 1200-1600 hrs. All subjects received 14 daily sessions, 50 minutes in duration, during which they received approximately 45mg of food on a fixed-time 60 second (FT60) schedule of reinforcement. Sessions were terminated and rats removed from the experimental chambers immediately after the 51st food delivery.

Subjects were randomly assigned to seven treatment groups of 8 rats each. The groups differed in regard to the food granulation sizes they received during the training sessions. One group (Group PEL) received 45mg Noyes pellets and served as a polydipsic control group to which the other groups, and existing literature, would be compared. The other groups received granulated food of particle-sizes of either 1.0 1.2, 0.8-1.0, 0.6-0.8, 0.4-0.6, 0.2-0.4, or 0.0-0.2mm . For simplicity, these groups are named according to their maximum particle-size. For example, the group receiving food of particle sizes ranging from 1.0 to 1.2 mm is referred to as Group 1.2, the group receiving food of particle sizes between 0.8 and 1.0mm is referred to as Group 1.0, etc. The groups were run through the two phases of the experiment as 8 overlapping replications, with each group being represented within a replication.

The rationale for choosing this range of particle sizes derives from the Beck, et al. (1988) study; they found that rats receiving granulated food composed of a range of particle sizes from 0.4-1.2mm on an FT60 schedule achieved

levels of polydipsia comparable to that of rats receiving pellets. Conversely, those receiving powder of particle size 0.0-0.4mm did not. The range of particle sizes chosen for the present experiment encompasses that within which Beck, et al., obtained their results.

The granulated food forms were prepared by mixing equal parts of Noyes Formula A granulated food (the same formula from which the pellets were made) and water into a mash, allowing this mash to dry, grinding the dried food in a blender, and sifting the resulting granulated food through a series of seives (W.S. Tyler of Canada, Ltd) in order to separate the desired particle sizes. The preparation of the mash was necessary because the stock form of food did not contain the larger particle sizes in adequate abundance, and also, it was felt that the homogeneity of the food would be enhanced by this process. Fresh food was made every 3-4 days, and once made, was kept in airtight plastic containers to ensure that there were no differences in moisture content between the different foods.

The only behavioural measure collected in Phase 1 was total session water intake for each rat on each session. Repeated measures ANOVA were applied to the data with groups as the between and sessions as the within. Heterogeneity of covariance was corrected for with the Geisser-Greenhouse correction factor. Duncan's Multiple Range (DMR) tests were used for comparison of groups within sessions and sessions within groups.

Phase 2.

No changes to the test apparatus were made for this phase of the experiment. Each subject received a single FT60 session, 50 minutes long, during which they received scheduled delivery of 45mg of the food granulation size appropriate to their group assignment. This session took place within 2 days of session 14 of Phase 1, and was videotaped to allow subsequent coding of behaviours. Since only one animal could be videotaped at a time, subjects were run in random order to control for time of testing effects; all were run between 0900-1600hr.

Seven behavioural categories were used: *drinking*, the licking of water from the water spout; *feeder-poke*, nose in the feeder hole; *rear*, raising the forepaws above a line 8cm above the floor; *groom*, licking, washing, or scratching itself; *locomote*, forequarters entering into any one of four quadrants that the chamber was divided into; *immobile*, sitting or lying without bodily movements; *investigate*, any movements not involved in the other behaviours, including mostly sniffing of the walls and corners of the chamber.

An observer coded for these behaviours from the videotapes using a microprocessor programmed to store the code of each keyboard entry. The session was divided into five 10-minute trials and the middle 6 min of each of these trials were coded. Therefore, there was a period of 4-min between each trial during which no observations were made.

Three measures were taken for each behaviour: bout frequency (BF), the number of nonconsecutive occurences of a behaviour per trial; percent-time (PT), the percentage of total time engaged in the behaviour within a trial; bout duration (BD), in which the score was a transformation of the absolute duration of a bout of behaviour. This transformation, which was used to normalize the duration scores, was the square root of the absolute bout duration in seconds plus 1. The transformation was also performed in order to enable direct comparison of the bout duration results of the present study with those of Beck et al. (1988), as the same tranformation was used in that study. In addition, the mean time spent engaged in each behaviour in each of ten 6-sec bins within each interfood-interval was computed in order to examine the pattern of behaviour within the interval.

Groups x trials x bins ANOVA were applied to the data with groups as the between, and trials and bins as the within-subject factors. Duncan's Multiple Range tests were used to compare the groups within trials, trials within groups, and groups within bins. Heterogeneity of covariance was corrected for using the Geisser-Greenhouse correction factor.

III. Results

A. Phase 1.

Figure 1 shows the mean volume consumed per session for each group. By session 14 asymptotic drinking appears to have been reached for most groups (Group PEL may still be increasing slightly). There were no significant differences in drinking within groups over the last five sessions. It is unlikely that any substantial increases in drinking levels would result from further training since the literature consistently shows that with rats food deprived to 80% body weight, and with appropriate schedules of reinforcement, polydipsia develops within 5-15 days (Falk, 1971). The 7 groups x 14 sessions ANOVA on volume consumed per session revealed a significant session main effect, $F(3.5,172.2)=115.88$, $MSe=916.94$, $p<.001$, group main effect, $F(6,49)=7.96$, $MSe=2.842 \times 10^4$, $p<.001$, and a group x session interaction, $F(21.1,172.2)=3.75$, $MSe=916.94$, $p<.001$. Nonsystematic inspection of the test chambers at the end of sessions revealed that water spillage was negligible, and would not have significant effect on statistical tests.

On session 14, which is taken as representative of asymptotic performance, Groups PEL, 1.2, 1.0, and 0.8 did not differ from each other significantly in volume drunk, Group 0.6 drank significantly less than did Group 0.8, Group 0.4 significantly less than Group 0.6, and Group 0.2 significantly less than Group 0.4, all $p<.05$. Table 1 shows

the mean session volumes for each group on session 14 as well as the variances and the ranges, the latter being particularly revealing of individual differences in response to the treatments. One of the rats in Group 0.8 drank only 10ml and one in Group 0.6 only 10.6ml, values that may be considered nonexcessive. In Group 0.4, five of the eight rats drank less than 10ml.

TABLE 1.

GROUP MEANS, VARIANCES, AND RANGES FOR SESSION 14 VOLUME INTAKE.

GROUP (mm)	MEAN SESSION INTAKE (ml)	VARIANCE (ml)	RANGE (ml)
PEL	23.6	0.8	15.5-33.1
1.2	21.2	1.8	14.1-30.3
1.0	22.8	1.7	13.1-31.5
0.8	20.0	0.9	10.0-28.5
0.6	17.4	0.5	10.6-28.7
0.4	10.9	0.8	4.4-20.0
0.2	6.0	0.6	3.4-8.6

The paired comparisons showed that all groups except Group 0.2 significantly increased water consumption over sessions, all $p<.01$. There were no significant group differences between session volume means for the first two sessions.

In summary, volume consumed at asymptote was not significantly different in rats receiving granulated food of particle-size larger than 0.6mm, or pellets. Further reductions in particle-size below 0.6mm resulted in less water consumption until at particle-size ranging 0.0-0.2mm there was no indication of excessive intake. Furthermore, rats receiving particle-sizes of 0.0-0.2mm did not increase water consumption from Session 1 values over the course of training, while all other groups did show increments over sessions.

B. Phase 2.

Immobilty occured with such little frequency (less than 1% of total time) that no data are reported for this behaviour.

Drinking:

A 7 groups x 2 sessions ANOVA comparing volume intake on session 14 of Phase 1 with that of the single session (session 15) of Phase 2 produced nonsignificant session and group x session effects (see Figure 1). Figure 2 shows the total session PT results for all behaviours, for each group.

Analyses were done with a groups x trials ANOVA.

It can be seen that rats trained on pellets and coarse granular food spent more time drinking than did those trained with finer powder; for PT groups main effect, $F(6,49)=11.70$, $MSe=3.11 \times 10^4$, $p<.001$. Likewise, the BF and BD of drinking were lower in the smaller granulation groups; groups main effects for BF drink, $F(6,49)=8.64$, $MSe=19.1$, $p<.001$, and for BD drinking, $F(6,49)=5.67$, $MSe=1.83 \times 10^4$, $p<.001$. These effects of granulation size on BF and BD drink are shown in Figure 3. Paired comparisons showed that Groups PEL through 0.6 did not differ significantly on any of the drinking measures, while Group 0.2 differed from the above groups on PT drinking, $p<.01$, BF of drinking, $p<.01$, and BD of drinking, $p<.01$. Group 0.4 differed significantly from Groups PEL through 0.6 on PT drinking, $p<.01$, and BD drinking, $p<.05$, and Group 0.4 also exhibited significantly fewer bouts of drinking than did Groups PEL, 1.2, and 1.0, $p<.05$. Group 0.6 approached significance on PT, BF, and BD drinking as compared to the pellet group only. The combined effect of fewer and shorter drinks by the animals in the small particle size groups likely resulted in the PT group differences.

The behaviours that showed significant group x trial effects are displayed in Figures 4, 5, and 6. A significant decline in PT drinking over trails within the session, trial main effect $F(3.2,155.1)=6.59$, $MSe=2152$, $p<.001$, is due to rats in Groups 1.0, 0.8, 0.6, and 0.4 decreasing the amount

of time spent drinking as the session wore on, whereas the rats in Groups PEL and 1.2 did not exhibit this decline, and Group 0.2 increased in PT drink over the session; group x trial $F(19,155.1)=2.47$, $MSe=2152$, $p<.001$. This PT interaction is largely due to a group x trial effect in BD, $F(18.8, 153.6)=3.68$, $MSe=3426$, $p<.001$, and is possibly contributed to by a BF group x trial $F(21.1,172.5)=1.59$, $MSe=1.82$ $p=0.0564$, which approaches significance. Figures 4-6 reveal the similarity in pattern of the group x trial effects on the three drinking measures.

Pairwise comparisons of trials within groups showed that PT drinking decreased significantly over the session from Trial 1 levels in Groups 1.0, 0.8, 0.6, and 0.4, and that it increased over trials for Group 0.2, all $p<.05$, while remaining stable over the course of the session in Groups PEL and 1.2. This decline in PT drinking relative to Trial 1 levels reached significant proportions for Group 0.4 by the second trial in the session, for Groups 0.6 and 0.8 by the fourth trial, and for Group 1.0, not until the fifth trial, (all $p<.05$). Over the session, relative to Trial 1 levels, BF and BD drinking decreased in Group 0.4, and BF decreased in Group 1.0. Groups PEL and 1.2 did not exhibit decrements or increments on any drinking measures over the session. Group 0.2 showed significant increases over the session from Trial 1 levels on BD and BF drinking, all $p<0.05$. Table 2 shows the individual rats' changes in percent-time engaged in drinking from the first trial of the

session to the last; the pattern is highly consistent. (The data for Group 0.2 rats are not shown as all rats in this group increased drinking rates by over 100% from Trial 1 to Trial 5, and some of these rats did not drink at all on Trial 1). Most rats exhibited decreases in drinking rate over the 50-minute session, and such decreases were less prevelant in rats receiving pellets or granular food of 1.0-1.2mm. The average relative decrement was much greater for rats in Group 0.4 than for other groups (-48.4% for Group 0.4, and -4.1 to -20.8% for the other groups).

TABLE 2.

PERCENT CHANGE IN TIME SPENT DRINKING ON FIFTH TRIAL OF SESSION 15 RELATIVE TO FIRST TRIAL FOR EACH RAT IN GROUPS PEL - 0.4. *

GROUP	PEL	1.2	1.0	0.8	0.6	0.4
	+21	+26	+26	+18	+23	-7
	+12	+7	-9	+5	-7	-9
	+1	+7	-17	-13	-16	-15
	+1	+7	-20	-29	-17	-59
	-16	-9	-21	-30	-23	-65
	-17	-10	-25	-33	-30	-68
	-22	-21	-27	-38	-32	-71
	-25	-40	-46	-46	-43	-93
Mean	-5.6	-4.1	-17.4	-20.8	-18.1	-48.4

* Data are excluded for Group 0.2 as all subjects increased drinking by over 100%, and some did not drink on Trial 1.

In sum, rats receiving scheduled pellets or granular food of particle size larger than 0.6mm spent the same amount of time drinking during the session, and this exceeded the amount of drinking by the rats receiving finer food. Differences in this regard were likely due mainly to shorter drinking bouts in the latter groups, as the group x trial effects on PT and BD drinking can be seen to follow similar patterns (see Figures 4 and 6), and significant group x trial effects were obtained for both measures. Animals trained on pellets or on food of particle-size larger than 1.0mm sustained their high rates of drinking throughout the session while animals receiving smaller food tended to decrease rate of drinking as the 50-min session wore on, unless they were receiving the finest 0.0-0.2mm powder, in which case they increased drinking rate over the session. Among those groups that showed decreased drinking rate over trials, these decrements tended to reach significant proportions relative to Trial 1 levels sooner, the smaller the granulation size was.

Other behaviours:

In Figure 2 it can be seen that drinking was not the only behaviour effected by the manipulation of food granulation size. The groups x trials ANOVA produced PT group main effects for all behaviours, but only investigate and feeder hole activity appeared to vary as a function of the decreased drinking exhibited by the small particle-size

animals; for PT feeder-poke the group main effect $F(6,49)=18.51$, $MSe=5.52 \times 10^4$, $p<.001$, for PT investigate $F(6,49)=4.30$, $MSe=4.14 \times 10^4$, $p<.001$, for PT rear $F(6,49)=4.68$, $MSe=1.54 \times 10^4$, $p<.001$, for PT groom $F(6,49)=2.85$, $MSe=1.39 \times 10^4$, $p=0.018$, and for PT locomote $F(6,49)=4.10$, $MSe=2280$, $p=0.002$. As granulation size and drinking decreased, the amount of time spent engaged in investigative behaviours did as well, while the amount of time spent with the head in the feeder hole increased. Group 0.2 spent less time in investigation than did any other group, $p<.01$, and Groups 0.4 and 0.6 spent less time in investigation than the pellet rats only, $p<.05$. There were no other differences in PT investigate between any other groups.

While PT rearing and grooming also tended to increase with decreasing particle size, the relationships are not as clear, as paired comparisons revealed that while Group 0.2 groomed significantly more than did any other group, all $p<.01$, there were no other significant group differences in PT groom. Group 0.2 also reared significantly less than did all other groups, all $p<.05$. The few other significant group differences revealed by the pairwise comparisons formed no discernible pattern.

The only behaviours that changed over the course of the session were drinking, rearing, feeder-poke, and investigation. Trial effects on PT rear, $F(3.4, 166.9)=4.85$, $MSe=2014$, $p<.001$, on PT head in feeder hole $F(3.3,$

161.9)=4.09, MSe=4052, p=0.006, and on PT investigate F(3.4, 167)=4.32, MSe=3275, p=0.004. Of these behaviours that produced significant trial effects, only for investigate was there no significant group x trial interaction. Thus, the data for investigate accross trials within the session are not shown. All groups increased the amount of time spent in investigation monotonically from Trial 1 through Trial 5. The group x trial effect on PT feeder-poke contains no discernable pattern, but the data for this effect are included in Figure 4. For feeder-poke, group x trial F(19.8,161.9)=1.68, MSe=4052, p=0.042.

A significant increase in PT rearing over trials is evident in Groups 0.4, 0.6, and 0.8 ($p<.05$). Groups 1.0, 1.2, and PEL did not change in time spent rearing over the session, nor did Group 0.2 (the latter animals spent less than 2% of the total session time rearing); PT rear group x trial F(20.4,166.9)=1.71, MSe=2014, p=0.034. Although the group x trial effects for BF and BD rear were nonsignificant, visual inspection of the within group changes in these measures across trials suggests that changes in both the number and duration of bouts of rearing produced the significant PT group x trial effects, since the general pattern of these changes are very similar for all three measures of rearing (see Figures 4-6). Cross-reference to the graph showing PT drinking over trials allows one to see that within a session, changes in drinking rate are mirrored by reciprocal changes in rearing.

Nonsystematic observation suggested that as food granulation size decreased, the time spent with head in the feeder hole between a food delivery and the subsequent drinking bout increased. These observations also suggested that most of the differences in the total amount of feeder-poke between groups were accountable for by group differences in this early-interval feeder-poke activity (i.e., consumatory behaviour) rather than by terminal (i.e., food anticipatory) head in the feeder hole activity.

In order to address the possibility that differences in early-interval feeder-poke activity associated with different food granulation sizes might account for the drinking effects another measure was collected from the videotapes: the amount of time with head in the feeder hole between the moment of each food delivery and the onset of the first subsequent bout of drinking, on intervals in which drinking took place. (Drinking occurred in over 94% of the interreinforcement intervals for rats receiving food of particles larger than 0.2mm). It would not be appropriate to call this an exact measure of time required to eat a food delivery, but it is likely related to consumption time requirements of the different granulated foods, and it is assumed to be a measure of the amount of oral and/or perioral activity preceeding each drinking bout (Beck, et al., 1988). Table 3 (p. 25) shows the group means for the average time with head in the feeder hole between food delivery and first subsequent drinking bout, on each of the

five trials, for all groups, except Group 0.2. Because rats in the latter group failed to drink after most food deliveries, and were just as likely to be drinking late in the interval as early in the interval, a reliable and meaningful measure of early-interval predrink feeder hole activity could not be obtained for these rats. Nonsystematic observations also indicated that animals in this group often consumed a food delivery in more than one eating bout. But, it must also be stressed that this problem was present only for the animals receiving powder of particle size 0.0-0.2mm. Animals in the other groups seemed consistent in consuming a food delivery in a single eating bout that commenced immediately after its presentation. Evidence for this later assertion comes from failure to find any food left in the dipper cups at the end of a session with rats receiving granulated food of particle-size greater than 0.2mm; sessions were terminated immediately after the delivery of the 51st food reward.

Correlational analyses within trials produced only nonsignificant correlations between the average time with head in the feeder hole between food delivery and first subsequent drinking bout, and the duration of that drinking bout. For Trials 1-5 the Pearson product-moment correlation coefficients, $r = -.23$, $-.20$, $-.19$, $-.22$, and $-.28$, respectively.

TABLE 3.

GROUP MEANS FOR AVERAGE AMOUNT OF TIME (seconds) WITH HEAD IN FEEDER HOLE BETWEEN FOOD DELIVERY AND FIRST DRINKING BOUT ON EACH TRIAL. *

	TRIALS					
	1	2	3	4	5	Mean
Group						
PEL	1.5	1.5	1.9	1.9	1.7	**1.7**
1.2	4.7	4.4	5.8	5.0	4.4	**4.9**
1.0	4.1	4.0	3.8	4.0	4.6	**4.1**
0.8	4.9	4.9	5.4	6.4	6.5	**5.6**
0.6	7.0	6.5	6.4	6.1	6.8	**6.6**
0.4	9.8	7.9	9.5	8.0	7.0	**8.4**

* Data for Group 0.2 is excluded because these rats did not consistently consume each food delivery in a single bout of eating, nor did they reliably drink after each food delivery.

In summary, as granulation size decreased, time spent engaged in feeder-poke tended to increase. These group differences were reflected in early-interval feeder-poke differences; there were only nonsignificant correlations between the time spent with head in the feeder early in an interval and the duration of the first subsequent drinking bout for that interval. Decreasing granulation size also tended to be associated with increases in time spent rearing and grooming, and decreases in time in investigation. Over

trials within the session time spent rearing tended to increase, and this effect was more pronounced for groups receiving finer granulation size (except for Group 0.2, which showed no changes in rearing over trials). Time spent in investigation increased over trials for all groups.

Interfood interval data:

The distribution of behaviours within the interfood-interval is shown for each group in Figure 5. The data are presented as mean percent time in each of the ten 6-sec bins that animals in a group spend engaged in each behaviour. Since group x trials x bins ANOVA revealed no significant three factor interaction effects for any behaviour, the interfood-interval data for each subject were collapsed over all six 1-min intervals within a trial, and over the five trials within a session. This provides a mean distribution of each behaviour, within the interfood-interval, for each subject that is based on the 30 coded interfood-intervals.

Main effects of bins and group x bin interactions were tested with a 7 groups x 10 bins ANOVA. All significant results of paired comparisons between groups for behaviours within bins were obtained at the alpha = .05 level.

Significant bin and group x bin effects were obtained on all behaviours. Bin main effects for drink $F(2.4,118.4)=178.32$, $MSe=6.63 \times 10^6$, $p<.001$, for head in the feeder hole $F(1.4,70.1)=41.03$, $MSe=2.07 \times 10^7$, $p<.001$, for

rear $F(2.7,131.5)=55.18$, $MSe=1.22 \times 10^6$, $p<.001$, for groom $F(3.9,189.7)=27.65$, $MSe=9.80 \times 10^5$, $p<.001$, for investigate $F(3.1,152.2)=87.10$, $MSe=3.76 \times 10^6$, $p<.001$, and for locomote, $F(5.5,271.8)=30.13$, $MSe=2.06 \times 10^5$, $p<.001$. The group x bin interaction effects were, for drink $F(14.5,118.4)=9.52$, $MSe=6.63 \times 10^6$, $p<.001$, for head in the feeder hole $F(8.6,70.1)=4.00$, $MSe=2.07 \times 10^7$, $p<.001$, for rear $F(16.1,131.5)=3.46$, $MSe=1.22 \times 10^6$, $p<.001$, for groom $F(23.2,189.7)=2.16$, $MSe=9.80 \times 10^5$, $p<.003$, for investigate $F(18.6,152.2)=3.06$, $MSe=3.76 \times 10^6$, $p<.001$, and for locomote $F(33.3,271.8)=6.10$, $MSe=2.06 \times 10^5$, $p<.001$.

The paired comparisons show the patterns of drinking and of feeder-poke within an interval to be almost identical for Groups PEL, 1.2, and 1.0, except for significantly more drinking and less feeder poke activity in the first bin by Group PEL animals. The same relative patterns of drinking are evident in Groups 0.8 and 0.6 as in Groups PEL, 1.2, and 1.0 in that drinking peaks in the second and third bins, but the peak level of drinking is lower in Group 0.8 (79%) than in Groups PEL, 1.2, and 1.0 (89-95%) and it is lower yet for Group 0.6 (68%). For Group 0.4 drinking peaks in the third bin as well but at a much lower level (44%). There were no significant differences in time spent drinking between any groups in bins 6-10. For all groups, little or no drinking occurred in the last 24 seconds of the interval.

For each of Groups PEL through 0.6 feeder-poke reached similarly low levels (less than 5%) while drinking was

peaking, but the lowest level of feeder-poke was reached sooner for Group PEL than for the others, and sooner for Groups 1.2 and 1.0 than for Groups 0.8 and 0.6, suggesting that as particle size decreases the amount of time required to eat a serving increases. For Group 0.4 feeder hole activity does not reach its lowest point (15%) until the fifth bin (i.e., almost halfway through the interval). The pellet control group displayed significantly less feeder hole activity in the first bin than all other groups. Groups 0.4 and 0.2 spent significantly more time in feeder-poke in the second and third bins than all other groups. Terminal feeder-poke activity (i.e., food anticipatory behaviour) began to increase for all but Group 0.2 in the fifth and sixth bins and reached similar peaks by the last bin of the interval, ranging from 52% (Group 1.0) to 69% (Group 0.8) in the tenth bin. All groups except Group 0.2 exhibited the same amount of feeder-poke behaviour between bins 4-10.

Several previous studies have suggested that eating and drinking behaviors compete for occupancy of the early portions of the interfood interval during SIP training (e.g., Reid and Staddon, 1982; 1987). In the present experiment the within bin correlation coefficienetween drink and feeder-poke were significant for the first four 6 second bins: for bin 1 $r=-.89$, bin 2 $r=-.90$, bin 3 $r=-.83$, and for bin 4 $r=-.56$, (all $p<.001$). This correlation proved to be nonsignificant for the other bins.

Group 0.2 differed dramatically from all other groups in regards to all of the aforementioned patterns of drinking and feeder hole activity. Feeder hole activity remained high throughout the entire interval and drinking only slightly increased towards the end of the interval (not statistically significant).

The amount of time spent rearing did not differ significantly between any of the groups in bins 1-3, or in bin 10. Between bins 5-9 Group 0.4 spent significantly more time in this behaviour than did any of the other groups, except group 0.6 in bins 5 and 6. Rearing occupied the middle portions of the interfood-interval in all animals, except for those in Group 0.2, who gradually increased rearing throughout the interval.

There were no significant differences in amount of grooming between Groups PEL through 0.4 in bins 1-3, or 7-10. The significant differences that occured in bins 4, 5 and 6 formed no discernible pattern, as Groups 1.0 and 0.4 tended to groom more during this time than did other groups. Group 0.2 grooming was significantly greater than that of all other groups in bins 1-3 and 8-10. Like rearing, grooming was most prevalent during the middle portions of the interval for all animals except those in Group 0.2.

There were no significant differences in investigation in bins 1-3 but, thereafter, the pellet group spent significantly more time in this behaviour than did most others, while Group 0.2 spent less time investigating than

all others during bins 5-7. The few differences between other groups that were obtained formed no pattern.

Group 0.2 spent the least time locomoting relative to all other groups in all but bins 1 and 10, and during bins 5-7 the differences between this group and all others were significant. There were few significant differences between other groups in any other bins. During the first bin the amount of locomoting decreased as food granulation size decreased. Group PEL spent significantly more time locomoting during bin 1 than did any other group.

In sum, drinking behaviour was confined to early in the interfood interval and closely followed consumption of the food reward in all but Group 0.2; there was very little drinking in the last half of the interval by any animals. There were group differences in the amount of feeder-poke at the beginning of an interval, but not in terminal feeder-poke. Rearing and grooming tended to occupy the middle portion of the interval, for all but Group 0.2.

IV. Discussion

The present experiment provided an independent replication of earlier findings from this lab reported in Beck et al. (1988); the development of polydipsia is retarded when rats are given finely powdered food on a schedule which readily produces excessive drinking with coarser food or with pellets. It also expands on those findings by demonstrating a graded particle size-response effect in which volume intake at asymptote is an inverse function of granulation size within a particular range (between particle sizes of 0.0 to 0.8mm). The lack of any significant differences between groups in volume drunk on the first two sessions indicate that the granulation size effect is not manifested until after the animals have had some experience with the schedule of delivery, consistent with the finding of Beck, et al. (1988).

Within the parameters defined in this experiment, the point at which decreasing particle size begins to signifigantly attenuate the development of polydipsia as measured by total volume drunk is at the 0.6-0.8mm range. Further decreases in granulation size result in even less drinking until at the 0.0-0.2mm range the rats drink an average of 6-7ml of water over a 50 minute session. This is similar to total water intake over the same time period when food deprived rats are allowed ad lib access to pellets. Lotter, Woods, and Vasselli (1973) found that rats food deprived and maintained at 80% of their pre-experimental

body weights drink an average of 7ml of water in one hour of free access to 45mg pellets. The volume consumed by the rats that received granular food smaller than 0.2mm in the present study was also similar to that of rats given the equivalent of fifty 45mg food portions in a massed-food condition of either pellets or fine powder. Beck, et al., (1988) found means of approximately 5ml consumed in a fifty minute session of either massed pellet or massed powder delivery.

By convention, schedule-induced drinking is considered excessive, and therefore polydipsic, if the volume consumed is significantly greater than that consumed when the same amount of food is delivered in mass (Roper, 1981). Therefore, when powder ranging in particle size from 0.0-0.2mm is delivered on an FT60 schedule the amount of water consumed per session at asymptote does not differ from the amount consumed when food is unscheduled, and therefore, drinking in these rats is not schedule-induced by the massed-food criterion suggested by Roper (1980; 1981). Appropriate massed-food and no-food control conditions were not implemented in this experiment, so the absolute degree of excessiveness of drinking cannot be ascertained. Still, the observation that volume drunk by rats receiving 0.2-0.4mm food was over twice that consumed by rats receiving similar food in massed food conditions, using the same apparatus, in the same lab (but in another experiment), suggests that drinking in 0.2-0.4mm rats can be considered

polydipsic by the excessiveness criterion.

The demonstration of a particle size-response effect as seen in Figure 1 supports the suggestion that the texture of the food was responsible for the original powder versus pellet effect on polydipsia first reported by Beck, et al. Thus, oral factors are strongly implicated in the control of SIP.

The results of Phase 2 further substantiate the food texture effect on SIP. For whatever reasons, finely ground dry food appears to be less effective than coarser granular food, or pellets, in eliciting protracted drinking bouts when delivered on an identical intermittent schedule. Results show that differences in overall volume drunk can be attributed to similar differences in the duration of individual drinking bouts, and to a lesser extent, to drinking bout frequency differences. Rats receiving finer food drank less because a typical food delivery elicited a drinking bout of shorter duration than did delivery of a pellet, or granular food of particle size larger than 0.4mm. Rats that received granulated food of particle sizes over 0.6mm were indistinguishable from rats receiving the standard 45mg food pellets in the prevelance of most behaviours, including the drinking measures, and in the distribution of these behaviours within the interfood interval, so the granulated nature of the food, per se, does not cause the polydipsia attenuating effect.

The consumatory response has similar topography for all the granulated food forms, coarse or fine, in that the food is licked up off the dipper cup in all cases. Obvious differences then, in the topography of the how different food forms were eaten cannot account for the effects. The possibility of differences in flavour or nutrient content of the various foods can be ruled out as all granulated foods were made from the same original food. For all groups, the food was delivered by an identical mechanism, and with the same associated auditory and vibratory cues accompanying its periodic operation. The observations in these experiments of increasing decremental effects on SIP as one descends through particle sizes below 0.8mm strongly suggests that this is the relevant dimension accounting for the original apolydipsic effect of food powder reported by Beck, et al. (1988).

Nonsystematic observations rule out the possibility that, at least for animals in Groups PEL through 0.4 (those receiving particle sizes of greater than 0.2mm), drinking may have been attenuated by failure to eat each reinforcer immediately after its presentation. The nonsignificant correlations between time spent with head in the feeder hole between a food delivery and onset of the first subsequent drinking bout (taken to be an approximation of time required to eat a food delivery) and subsequent drinking bout duration suggests that the powdered food effect cannot be attributed to consumption time requirements imposed by

granulated foods, or to the amount of oral and perioral activity associated with delivery of the different granulated foods. This adressed directly one of the hypotheses suggested by Beck, et al. (1988); they found that there was a reciprocal relationship between the amount of oral and perioral activity associated with a textural form of food and the amount of water drunk by animals receiving scheduled delivery of that food. It was suggested that this factor may account for the apolydipsic effect of powdered food. The present findings suggest that this is not a causal factor (but see Section VI, p.70, for an alternative suggestion) as the amount of early-interval feeder-poke activity did not increase over trials for any group (see Table 3), while drinking behaviours were declining for most animals.

All groups that received granular food of greater than 0.2mm particles exhibited patterns of drinking that are characteristic of SIP. That is, the levels of drinking developed gradually over sessions (Staddon, 1977), and there was usually a single bout of drinking following soon after the delivery and ingestion of a reinforcer (Staddon and Ayres, 1975), and which occupied the early part of the interfood interval (Staddon, 1977). Also, the volume consumed in a single session of scheduled delivery exceeded that consumed in a massed food condition of similar duration (Beck, et al., 1988; see above). Volume intake in rats receiving the 0.0-0.2mm food was similar to that of rats

receiving massed food presentation or ad lib food, (cf. Lotter et al, 1973, and Beck, et al., 1988), drinking was not reliably elicited by each food presentation, and when drinking did occur it was just as likely to occur late in the interfood interval as early (see Figure 5). There was only a nonsignificant increase in volume intake over sessions for these animals. These latter results indicate that drinking was not schedule-induced in animals receiving granulated food smaller than 0.2mm. Nor were any other behaviours apparently controlled by the schedule, as the flat lines that represent temporal allocation of behaviours within the interfood interval for Group 0.2 in Figure 5 indicate.

At least one aspect of the drinking induced in rats by granular food smaller than 1.0mm was slightly atypical of rats trained to be polydipsic by the delivery of pellets: These animals tended to show some degree of satiation of drinking over the course of the session, while drinking in those receiving food particles larger than 1.0mm, or pellets, remained similarly excessive throughout. The smaller the granulation size of the food was, the sooner within the session significant declines in drinking tended to occur. SIP in pellet trained rats has been noted for its persistence over sessions of relatively long duration (Falk, 1971). Keehn and Riusech (1979) trained rats on FI60sec pellets for sessions of 7 hours duration, and observed no decrements in water spout licking until more than two hours

on the schedule had passed. Between the second and fifth hours there were declines in lick rate. However, Freed and Hymowitz (1972) observed steady declines in lick rates over a one hour session of FI60sec for single food pellets. Reid and Staddon (1982) also found decrements in time spent drinking on FT30sec and FT120sec schedules over the course of 20 minute sessions. The rate of decline in drinking was greater for rats receiving 6 pellets than for rats that received one pellet per delivery. The present study is, to the best of the author's knowledge, the first demonstration that the rate of decline in schedule-induced drinking can be influenced by factors other than the schedule employed or the magnitude of reward.

Reductions in drinking accompanying reduced food granulation size appear to be accompanied by nonselective increases in other behaviours. In the present experiment, group means for percent of total session time engaged in rearing, grooming, investigating, and feeder-poke all increased as the measures of drinking decreased. The increase in feeder-poke behaviour seemed to be comprised of increases in early-interval (assumed to be largely consumatory) feeder hole activity rather than in late-interval (food anticipatory) increases in feeder activity. This is similar to observations made by Reid and Staddon (1987) who found increases in early-interval head in feeder behaviour with increases in reward size, but no differences in terminal head in feeder behaviour. Increasing

meal size in their study also led to decreases in time spent drinking. Inspection of Table 3 reveals that there were no increases in early-interval head in feeder activity over trials within a session, for any group, nor were there across trials increases in total feeder-poke activity (Figure 4), even though most groups showed decrements in drinking over trials. Therefore, reductions in drinking measures that occured within a session cannot be attributed to simple displacement by increasing feeder behavior. Only when session totals for feeder related activity are compared between groups does there seem to be a reciprocal relationship between this behaviour and drinking behaviours.

Inspection of the interfood-interval data shows that rearing and grooming increased in prevelance during the period of the interval vacated by the shorter drinking bouts of the rats receiving finer food, that is, between 6 and 30 seconds after food delivery. Also, rearing increased across trials within the session in those groups that showed across trials decreases in drinking. In sum, as drinking decreased due to decreasing food particle size, it was mainly those behaviours that Staddon (1977) described as 'facultative' behaviours (those behaviours that are not induced by the schedule, and that tend to occupy the middle portion of the interval) that increased in response. Both grooming and rearing are facultative activities and both tended to increase with decreases in drinking, although this effect was greater with rearing. This latter observation contrasts

with those of Roper and Nieto (1979) who found selective increases in grooming as levels of polydipsia were attenuated by increasing body weight. Presumably, as the amount of time engaged in interim activity (early interval, schedule-induced; Staddon, 1977) decreases, the resulting increase in time available for other behaviours is filled with facultative activities (Staddon and Ayres, 1975). Since no particular behaviour replaced drinking as an interim behaviour early in the interval, except oral and perioral activity which was likely forced to by the consumption requirements of the granulated foods, then it might be concluded that schedule-induced drinking was not replaced by an excessive schedule-induced other behaviour.

It seems that attenuated SIP is a direct result of presenting granular food of particle size smaller than 0.8mm, and is not a secondary effect due to increases in another behaviour produced by food of this type. Unfortunately, in the present experiments there were no massed-food or no-food control conditions conducted by which the excessiveness of other behaviours could be assessed. However, it is obvious from the data that any increases in behaviours other than feeder hole activity, that accompany decreases in drinking, are too small to be simply substituting for excessive drinking. Appropriate massed-food and no-food control conditions would have had to be run in order to ascertain whether feeder-poke activity was excessive by standard criteria (Roper, 1981).

There are a number of implications that the present results hav for some theories of SIP that are, or have been, in vogue. First, the apolydipsic effect of finely granulated powdered food is quite incompatable with the once popular 'dry-mouth' hypothesis of SIP (Stein, 1964). This theory holds that SIP is a exaggeration of water intake necessitated by the drying of the animal's mouth due to intermittent delivery of small amounts of food. Presumably, the animal must drink after every pellet delivery in order to sufficiently lubricate its oropharyngeal passage, and allow swallowing of the reinforcer. There is no obvious reason why dry powdered food would not also elicit drinking if this were indeed a fuction of SIP. Tests for moisture content of the different granulated food forms were not conducted, but any differences in this regard would be minimal since all food was separated from the same stock, and was kept in airtight containers. Appropriate tests for moisture and nutrient content of the different food granulation-sizes would be required to exclude them as being at least partially involved in the granulation effect on drinking.

A study by Falk (1967) in which excessive drinking was produced in rats by the scheduled delivery of liquid monkey chow would seem to argue against the idea that coarsely textured food is necessary for the generation of SIP. However, Hawkins, Schrot, Githens, and Everett (1972) attempted to replicate Falk's findings with liquid monkey

chow using larger groups of rats (10 animals as opposed to just the 2 used by Falk) and although some of their rats did drink excessively, some also drank negligible amounts, and the group mean for water intake was significantly lower than that for a different group of rats delivered pellets on the same intermittent schedule. Very similar results were found in the present experiment when drinking with the more finely ground food is compared with that with much coarser food or with pellets. Just as Hawkins, et al. found, data from individual rats reveal considerable range in the treatment effects (see Tables 1 and 2). But Falk's results are more likely attributable to the high salt content of the liquid food he used (6.5% salt). A number of liquid foods that do not normally produce SIP will do so if adulterated with salt in concentrations over 7% (Poling, Krafft, Chapman, and Lyon, 1980).

It would also be difficult to subsume the texture effects on SIP under a model based on adventitious reinforcement (Clark, 1962). The temporal proximity of reinforcer delivery to drinking was the same for animals receiving either coarse or fine food, that is, there was equal delay between cessation of drinking and the delivery of the next reinforcement (see Figure 5). Also, regardless of the form of food delivered, it remains a primary reinforcer for food deprived rats. There seems, therefore, no reason why drinking would be reinforced by coarse, but not by fine food.

Also, for similar resons, it is difficult to explain the texture effect by a model of SIP based on the idea of drinking as a displacement activity (Falk, 1971). The latter view has it that schedule-induced drinking results when a highly motivated consummatory activity is thwarted, and its expression reflects the competing responses of concurrent approach and avoidance of the situation. It is presumed that hungry rats are frustrated when they are forced to wait long periods between the presentations of food portions that require only seconds to consume. These animals are compelled to escape from this aversive situation, but they are hungry, so there are also reasons why they should stay and receive the next food delivery. In the present experiments, thwarting of eating behaviour occured with the same frequency (i.e., once each minute) regardless of the granulation size that was delivered Furthermore, the magnitude of this thwarting effect would be expected to be the same for all subjects because the amount of food delivered was the same (Wuttke and Innis, 1972). These two considerations are problematic for an account of the food granulation effect in terms of the displacement activity model.

However, it could be that pellets and coarse food are preferred forms of food relative to a finely powdered form. The implications that this possibility has for the displacement activity model of SIP is that thwarting of the consummatory act would be of lesser psychological magnitude

with the "less rewarding" finely granulated food, and the result would be less frustration induced drinking. Pelletted foods have been found to be preferred over powdered food by rats, as measured by amount consumed in a choice situation using foods of various flavours (Naim, Brand, Christensen, Kare, and Buren, 1986). Falk (1967) found SIP to be directly related to the palatability of the scheduled food. In order to ascertain whether there was a relationship between quality of reinforcer used in the present experiment, and the amount of elicited drinking, appropriate preference tests would need to be conducted. If such preference tests were done, and they revealed parallels between rewarding efficacy of granulated food forms and their ability to elicit polydipsia, then the motivation/displacement activity interpretation of SIP would be supported.

Another factor that renders interpretation of the present results in terms of motivation unviable is that there was no difference between groups in the amount of terminal feeder hole activity. If one form of food had greater incentive value for the animals than another, then the resulting increase in motivation would be expected to reveal itself in enhanced food anticipatory behaviour (Nieto and Posadas Andrews, 1984). Hence, it is difficult to account for the present results with an unmodified version of the displacement activity model of SIP.

However, the current findings regarding the effect of food texture can be explained in an intuitively appealing

way if approached with the view that SIP is a form of sensitized behaviour. According to current theory of response sensitization, increments in an elicited response occur with repeated presentation of the eliciting stimulus. SIP resembles sensitized behaviour in this regard (Wetherington, 1982).

The degree to which sensitization occurs is primarily a function of the frequency and intensity of the repeated stimulation (Groves and Thompson, 1970; Petrinovich, 1984). Generally, greater levels of response sensitization will follow repeated presentation of a high intensity stimulus than a low intensity stimulus. Conversly, when a low intensity stimulus is used, the process of response habituation will predominate and the net behavioural output will decline as a result. The two processes of sensitization and habituation are presumed to occur independently but interact to produce the final level of behavioural output. Both the incremental and the decremental processes are a direct function of stimulus frequency, but net sensitization will prevail when the situation is one of high intensity stimulation of moderate to low frequency (Groves and Thompson, 1970). In this case, the occurence of concurrent response habituation is minimized, and the sensitization process is allowed to be expressed more fully than if frequency of stimulation is high. Section VI contains description of current theories of response habituation and sensitization, as well as discussion of a sensitization

account of other SIP data.

In the proposed model of SIP as a sensitized behaviour, the eliciting stimulus is the periodic food reinforcer, and the elicited behaviour is drinking. It may be that a relevant dimension on which the intensity of a food stimulus as a drink eliciting stimulus to a rat can be rated is the texture gradient. Any oral or ingestive behaviour might substitute adequately for drinking, such as pica, or airstream licking, but the availability of a water spout dictates that this will be the prepotent ingestive activity (Staddon and Simmelhag, 1971).

The appeal of these assumptions is bolstered in light of recent demonstrations of the necessity of oral somatosensation for the initiation and control of ingestive behaviour (Miller, 1981; Zeigler, Semba, Egger, and Jacquin, 1982). Miller deafferented rats to various degrees of oral somatosensory impairment and found that the greater this impairment, the less investigative activity, eating bouts, and water spout exploration a rat was likely to partake in. The amount of ingestive behaviour, in short, was directly related to the amount of orosomatic stimulation the animal was capable of receiving. Zeigler, et al., showed that mechanical stimulation of oral and perioral areas in the rat elicits sequences of oromotor responses normally involved in ingestive behaviour.

In the present experiments, the frequency of orosensory stimulation in the form of a food reinforcer was constant

for all subjects (once per minute) so frequency of stimulation would not be expected to affect sensitization. But the intensity of the stimulation was varied by manipulating the texture of the food. Rats receiving the less textured powder food would be expected to be getting less intense orosensory stimulation, because the degree of mechanical stimulation in the oral cavity would *presumably* be less with smaller food particles. For this reason, they may exhibit less responsiveness to features of the environment that evoke ingestive behaviours, such as the water spout. Jacquin and Zeigler (1983), found decreased responsiveness to ingestion associated environmental cues in rats that were subjected to trigeminal deafferentation and which, thereby, suffered orosensory impairment. Their results indicate the critical role of orosensory inputs in initiation and maintenance of drinking.

The current working hypothesis is that periodic and repeated mechanical stimulation of the oral cavity in rats sensitizes, and thereby enhances, the animal's propensity to engage in ingestive activity, of which drinking is a type. Two predictions made by this model, *with the assumption that texture is a valid measure of food stimulus intensity*, were borne out in the present results. First, the most obvious prediction is that if schedule-induced drinking is a sensitized behaviour, then this sensitization should be greater with a coarser granulated (i.e., higher intensity) food stimulus. The primary effect of food granulation size

was that of more post-food drinking in animals that received coarser food or pellets, and this effect is taken to reflect a greater degree of long-term sensitization of the food elicited drinking response (see Section VI, p. 65, for a description of long-term and short-term forms of sensitization and habituation). Gradual incremental effects caused by repetitive stimulation, and not obviously accompanied by concurrent decremental processes, have been reported previously. For example, Franzisket (1963) obtained prolonged sensitization of the frog wiping reflex over the course of several daily sessions of repeated tactile stimulation. Secondly, if the dual-process model is adhered to then there should be at least some degree of response habituation that occurs with the repeated stimulus presentation. Whether or not this habituation will be great enough to noticably counter the simultaneously developing sensitization depends on, among other things, the intensity of the eliciting stimulus. Habituation will be greater, and sensitization will be lesser, when the stimulus used is of lower intensity (i.e., food of smaller granulation size). Indeed, the decrements in drinking rate over the session in rats receiving finer food resembled habituation of a sensitized response. (Since these latter animals were still polydipsic, but to a lesser degree, it would be proper to consider their post-food drinking as *less* sensitized, rather than as unsensitized). Admittedly, these observations were based on a single session, but a strong consistency in the

patterns of relative changes in drinking rate over the session for particular rats is seen in Table 2.

The habituation of schedule-induced drinking would be interesting because one of the primary charactreristics of SIP is its persistence (Falk, 1971). The dual-process theory states that the initial (short-term) sensitization process accompanying repeated stimulation should begin to decay (i.e., habituate) if the series of stimulus presentations continues long enough. Less sensitized behaviour will begin to noticably decline sooner than will more sensitized behaviour. It has been reported that drinking produced with standard 45mg pellets does show decrements within the course of a session if session duration is long enough (Keehn and Riusech, 1979). In the present experiments, a decline in drinking was evident within a 50 minute session for rats that are hypothesized to have been less sensitized due to the intermittent delivery of a lower intensity stimulus, than the pellet receiving rat. Moreover, the onset of this decline was earlier for rats receiving food particles of 0.2-0.4mm than for those receiving 0.4-0.6mm, or 0.6-0.8mm particles (see Figure 4), and which, in turn showed earlier declines than rats receiving 0.8-1.0mm food. Therefore, rate of habituation appears to be greater, the less intense the eliciting stimulus, as the model predicts. In light of this consideration, it may be that significant differences in drinking would be observed between groups receiving the larger granular foods if session length was increased,

because the effects of differential rates of declines in drinking would be allowed greater expression.

In summary, the present study examined the effects of food granulation size (texture) on the development of schedule-induced drinking. The primary findings were: 1) Decreasing food granulation size results in attenuation of SIP development. 2) Asymptotic effects of decreased granulation size are decreases in volume consumed within a session, time spent drinking from the water tube, duration, and to a lesser extent frequency, of post reinforcer drinking bouts. 3) The patterns of attenuated drinking in rats that received fine granular food conformed to those characteristic of polydipsia. 4) The finest granular form of food used (0.0-0.2mm particles) did not produce schedule-induced drinking. 5) No other behaviour became excessive in place of excessive drinking in rats receiving finely granulated food. 6) Rats receiving finely granulated food decrease the time they spend drinking over a session, while those receiving coarser food do not. The results of the present study have been interpreted as supportive of the view of SIP as a sensitized behaviour. If the assumption is made that the texture of intermittently delivered food determines its intensity as a drink evoking stimulus then the results of this manipulation fits certain predictions made by current theories on response sensitization and habituation. Evidence from trigeminal deafferentation studies have implicated the role of oral somatosensation in

the control and initiation of ingestive responses and in light of these demonstrations, the assumption regarding the importance of food texture in eliciting drinking behaviour is given some independant validity. The view of SIP as a sensitized behaviour provides a working hypothesis for future research concerning the effects of food texture on SIP.

V. SIP LITERATURE REVIEW

This section contains an account of most of the major findings of the past twenty-five years of SIP research, as well as a breif description of the theories that have been developed to explain these phenomena. As such, this review does not include discussion of the results of the present study, and is intended to provide the background information necessary for some of the arguments put forth in Section VI.

Falk (1961a) was the first to report that hungry rats consume large amounts of water while bar pressing for food on an intermittent schedule of food delivery. In his experiment rats responded on a variable-interval schedule in which a lever press produced a small food pellet on the average of once every 60 seconds (VI60). Falk found that the rats would begin drinking water immediately after consuming each pellet. The cumulative result after 3.17 hours on this schedule was that the rats drank over 3 times their pre-experimental daily water intake. This phenomenon was subsequently termed "schedule-induced polydipsia" (SIP) to denote the excessiveness of the behaviour as well as its dependence on intermittent delivery of a reinforcer.

SIP has been demonstrated with a number of species including rhesus monkeys (Schuster, 1966), pigeons (Shanab and Peterson, 1969), and humans (Kachanoff, Leveille, McClelland, and Wayner, 1973), and rats (e.g., Beck, et al., 1988; Falk, 1961a,1961b). Thus, there appears to be nothing unique to demonstration of polydipsia in the laboratory rat.

Since Falk's discovery of SIP, several researchers have added to the list of factors that influence the amount of water that rats imbibe in under conditions of intermittent food delivery. It is known, for example, that a response-contingency is not necessary for the generation of the effect. Falk's (1961a) original account of SIP utilized a variable-interval 60-second schedule. Since it seemed possible that SIP might be a displacement from an operant system to another response, Falk examined the effect of a noncontingent variable-interval 60-sec (VT60) schedule and found that the acquisition of SIP was unaffected (Falk, 1961b). SIP has also been obtained with fixed-ratio (FR) schedules (e.g., Falk, 1961b), and by several researchers using fixed-time (FT) schedules of food delivery (e.g., Roper and Nieto, 1979; Wayner and Greenberg, 1973). It therefore appeared that SIP was the result of intermittency of food delivery per se, and that it occurred whether or not an operant response was required for reinforcement.

Several experimenters have examined the effects of reward size on SIP, but their studies have produced conflicting results. Flory (1971) and Falk (1969) both found that the amount of drinking per reinforcement delivery was greater when two pellets were delivered than when only one was. Rosenblith (1970) obtained a greater level of polydipsia with 250mg pellets than with 45mg pellets. However, despite the evidence for a positive relation between reward size and drinking, Freed and Hymowitz (1972),

and Yoburn and Flory (1977) obtained decreased drinking with increases in reward size. Lotter, Woods, and Vasselli (1973) found that SIP was readily obtainable with reward sizes of 1 or 4 pellets, but not with 12 pellet rewards. In all of these aforementioned experiments the size of the food reward was varied *between* sessions. When the number of 45mg pellets per delivery is varied between 1 and 9 pellets, and this manipulation is made *within* a session by randomly assigning different reward sizes to different intervals within the session, the amount of drinking after a food delivery is inversely related to the size of the delivery (Reid and Staddon, 1987). In an earlier experiment, Reid and Staddon (1982) presented extra food at the end of occasional fixed intervals within a session of FT pellet delivery and found that the extra food evoked less drinking. This attenuation of drinking was limited to the intervals containing the extra food, and was attributed to a concommitant increase in food related behaviors during these intervals.

Whatever the precise relation between food magnitude and SIP happens to be, it is now clear that session totals of water consumed are not a useful measure of such effects (Reid and Staddon, 1982). This is because the effects of food size on total amount of drinking presumably depends on both the interval length chosen as well as the duration of an experimental session. It has been shown that rats receiving 6 pellets per delivery on a FT30sec schedule will begin the session drinking at a greater rate than will rats

on the same schedule that receive only single pellet deliveries, but by the end of a 20 minute session the rats receiving six pellet deliveries will have decreased their drinking rate to levels below those of the single pellet rats (Reid and Staddon, 1982). The exact nature of the effects of food magnitude on SIP remain uncertain, although the bulk of the evidence suggests that, all else being equal, larger reward size produces less schedule-induced drinking.

One feature of SIP that is considerably less controversal is the observation that induced drinking increases with increasing food deprivation level, or decreasing body weight (Falk, 1969). Freed and Hymowitz (1972) confirmed this effect of body weight deficit. However, though reduced body weight may enhance the robustness of polydipsic effects, it is not a necessary condition for obtaining excessive schedule-induced drinking. Wayner and Rondeau (1976) found excessive drinking in rats that were trained on a FI60sec schedule at 80% ad lib body weight, and later returned to 100% ad lib weight. Although drinking in recovered rats was considerably less than when these same rats were food deprived, it was still significantly greater than in a group of rats trained on a schedule at ad lib body weight that were never food deprived. In another study, it was not even necessary to initially train subjects at reduced body weight in order to generate polydipsia (Roper and Nieto, 1979). Although Roper

and Nieto also found that SIP was an increasing function of decreasing body weight, rats that were kept at ad lib body weight still drank more under conditions of intermittent food delivery than in a massed-food control condition, indicating that an intermittent schedule can produce some degree of polydipsia even in satiated rats. Food deprivation seems to reliably enhance the acquisition of SIP, but it is not a necessary condition for production of the effect.

One of the most critical factors influencing the degree of SIP acquired under conditions of intermittent food delivery is the interfood interval used. The function relating SIP to interval length is a bitonic one in which increasing interval length produces greater levels of polydipsia up to a point, after which further increases produce less drinking (Falk, 1966). Flory (1971) trained rats to bar press for pellets on FI schedules ranging from FI1sec to FI480sec. He obtained little water consumption on schedules shorter than 5 seconds, and progressively more intake as interval length was increased between 5 and 120 seconds. Volume consumed decreased monotonically with further increases in interval length. A similar bitonic function was obtained when two pellets were delivered at the end of each interval instead of only one pellet. Wayner and Greenberg (1973) also reported an inverted-U shaped function relating fixed-time interval length to the number of licks at a water spout. Licking increased as interval length increased between 1 and 4 minutes, after which it decreased

as interval length increased to 5 minutes. Experiments in which the interval length is increased while the number of reinforcements obtained is held constant will necessarily require increases in the duration of sessions. Conversely, when session length is held constant there will be fewer food deliveries with increases in interval length. However, when either session duration or number of reinforcements within a session are maintained at constant values, the bitonic function relating interfood interval and SIP measures maintains (Falk, 1971).

There are several other factors which have been shown to have an effect on levels of schedule-induced drinking. Freed (1971) found that the volume of water ingested decreased with decreased nutritive content of food pellets. Falk (1967) manipulated the palatability of scheduled food and found that there was a positive relation between SIP and palatability of the reinforcer. Flory and O'Boyle (1972) demonstrated that if the availability of water to an animal is restricted to the later portions of the interfood-interval, SIP is attenuated slightly, though not eliminated completely. A number of pharmacological agents have also been tested for their effects in the SIP paradigm (Wallace and Singer, 1976, provide a review).

But, regardless of the accumulation of facts about SIP an adequate explanation of the processes involved in the generation and maintenance of this peculiar phenomenon remains elusive. Many attempts have been made invoking

either physiological or behavioural explanations but none can account for all the data (Staddon, 1977, and Wetherington, 1982, provide good reviews).

Researchers initially attempted physiological explainations of SIP. One factor that appeared critical for the production of SIP was that the reinforcer delivered was dry food. Stein (1964) was a strong advocate of the "dry mouth" hypothesis of SIP which held that the excessive drinking engendered by the intermittent schedule is necessary in order to allow the animal to sufficiently lubricate its oropharyngeal cavity and allow repeatedly presented portions of dry food to be swallowed. Stein (1964) demonstrated that substituting sweetened condensed cow milk for dry pellets under conditions of intermittent delivery did not produce polydipsia. Similarly, Stricker and Adair (1966) failed to obtain SIP with vegatable oil as the reward. But, Falk (1967) did demonstrate polydipsia using liquid monkey chow as the reinforcer. This finding was taken as conclusive evidence that SIP was not due to a dry mouth. Further evidence against the dry-mouth hypothesis comes from the observation that wetting the rats mouth by means of an intra-oral tube does not stop polydipsia (Falk, 1971), unless the volume of water orally infused is equivalent to the amount that would normally be consumed in an SIP session (Kenny, Wright, and Reynolds, 1976).

One of the first behavioral hypotheses that attempted to explain SIP suggested that it may be an adventitiously

reinforced superstitious behavior (Clark, 1962; Segal, 1965). In a 1948 paper B.F. Skinner described an experiment in which he showed that the mere presentation of food to a hungry pigeon was enough to produce operant behavior, even though there was no response contingency involved in the delivery of the reinforcer. The pigeons in that experiment came to emit idiosycratic and stereotyped behaviors that were temporally correlated with food delivery, and the interpretation of the processes involved in generating this "superstitious" behavior was made in terms of the Law of Effect: Since there was certain to be behavior of some sort occuring at the moment of food delivery, such behavior was 'adventitiously' reinforced, and therefore, its reoccurrence increased in probability, thereby increasing the probability that it would appear in close temporal proximity to the reward, only to be further reinforced. Clark (1962) and Segal (1965) thought that SIP may be produced in this same manner.

There are several lines of evidence that mitigate against an explanation of SIP in terms of adventitious reinforcement. First, superstitiously maintained behavior is characterized by its idiosyncratic nature and by shifts in the topography of the response, while SIP develops quite rapidly and is quite stable once it is established (Falk, 1969). Secondly, If SIP were superstitiously maintained behavior then it would be expected that drinking would occur late in the interval, in temporal proximity to, and

preceeding the delivery of the food reward. In fact, one of the characteristics of schedule-induced drinking is that it *follows* rather than preceeds the delivery of the reinforcer (Stein, 1964). Third, Falk (1964, cited in Wetherington, 1982) has demonstrated that polydipsia can be generated by a schedule with a contingency that requires that drinking not occur within 15 seconds before a bar press in order for the bar press to produce food. Fourth, polydipsia can be produced with FR schedules, when the pause in operant responding that is introduced by post-pellet drinking actually increases the time to the next reinforcer delivery (Falk, 1969). In sum, the adventitious reinforcement hypothesis has not fared well as an explanation for SIP.

In response to this failure of the adventitious reinforcement hypothesis, Falk (1969) proposed a motivational account of SIP. Simply stated, the idea is that the more motivated the animal is by such factors as food deprivation, or reduced body weight, and the more motivating the situation is (incentive, frequency, magnitude, quality of food), the greater the tendency to drink (Staddon, 1977).

Central to Falk's motivational account of SIP is the assumption that the intermittent delivery of small amounts of food to the food-motivated rat constitutes a situation in which the animal has its consummatory drive repeatedly thwarted. The result of this thwarting of the drive is the appearance of a displacement activity. Falk (1971) describes displaced behavior as "a response sequence which is

ordinarily a function of variables other than those which presumably dominate the current situation." (p.585). The dominant variable in an intermittent schedule of food delivery to a hungry animal is the food, to which the primary response is eating, not drinking. The drinking response is assumed to arise as a result of frustrative non-reward that is inherent in the intermittency of the food delivery (Falk, 1971).

The evidence relating increases in SIP to decreases in body weight is extensive, and it supports the motivational hypothesis. As previously mentioned, SIP appears to be a direct function of reinforcer palatability (Falk, 1967), and there is some evidence of increases in schedule-induced drinking with increases in food reward size (e.g., Rosenblith, 1970; Flory, 1971). Even the contrary evidence that increasing reward magnitude decreases drinking (e.g., Yoburn and Flory, 1977) does not seriously damage the motivation hypothesis. Although increasing the food magnitude should result in greater motivation to eat, the thwarting of which should then be greater, it may also be the case that with larger reward sizes the consummatory response is allowed a greater degree of expression each time a reinforcer is delivered before being thwarted, thereby attenuating the hypothesized frustrating effect of the intermittent schedule. There is, in fact, little data that makes a compelling arguement against the motivational, frustrative nonreward hypothesis.

Twenty-five years of research has shown that there are several factors which influence the development SIP. Among the most potent of these are degree of food deprivation, scheduled interfood interval length, and magnitude of the food reward. Breifly, levels of excessive schedule-induced drinking appear to increase with increasing food deprivation, and to decrease with increases in the food reward size. The relationship between SIP and interfood interval is a bitonic one in which increasing the interval length results in enhanced drinking up to a point, whereafter further increases in interval length lead to less drinking. Physiological accounts for SIP, such as the 'dry-mouth' hypothesis, have been, thus far, unable to account for all of the data. Behavioral accounts based on adventitious reinforcement of superstitious drinking behaviour have also failed. However, a theory based on the idea that SIP is a displacement activity, and that levels of induced drinking are positively related to the motivation to eat, has fared slightly better. Recently, it has been proposed that SIP might be a form of nonassociative learning, namely behavioural sensitization. There is ample evidence to support this latter hypothesis (see Section VI.).

VI. SENSITIZATION THEORY AND THE FITTING OF SIP DATA

Over the past two and a half decades several people have attempted to provide an explanation for the genesis and maintenance of SIP. For the most part these attempts have been vested in either behavioural or physiological terms, but seldom both. Initial theories invoked physiological functions such as dry-mouth, impaired renal function, or homeostatic mechanisms such as temperature regulation (Falk, 1969). Such theories failed and behavioural models based on operant or classical conditioning were put forth, only to similarly fail to account for all of the data. Only quite recently has it been suggested with any clarity that SIP might be a form of nonassociative learning (Wetherington, 1982). The view is that SIP may be a manifestation of sensitized behaviour. Wetherington points out that, like more typical sensitization paradigms, SIP training involves repeated presentation of a stimulus (food in this case) and the behavioral change is a progressive enhancement the magnitude of a particular response (drinking in this case).

The idea that SIP is a form of nonassociative learning requires some justification for believing that it is not an instance of associative learning. A powerful demonstration against the latter view was made in the Beck, et al. (1988) study. They found that in a condition in which food delivery was omitted on 30% of intervals on an FT60 schedule, polydipsic rats did not drink during these intervals. If SIP were either an operant behaviour reinforced by food

delivery, or a simple unconditioned response to food delivery, amenable to temporal conditioning, then gradual, not immediate extinction of the response would be expected in the condition of randomly ommited food deliveries.

The results of the present experiment can be interpreted as supportive of the view of SIP as a sensitized behaviour. In addition, much of the existing data on SIP can be easily fitted to the sensitization model. Following a breif overview of current sensitization and habituation theory, the fit of existing SIP data to this model will be discussed.

A. Dual-process theory:

Groves and Thompson (1970) outlined a dual-process theory based on their research with spinal cat. The model was further updated by Thompson, Groves, Teyler, and Roemer (1973). The theory contains two inferred processes, habituation and sensitization, that predict and describe the course of changes in magnitude of response to a repeatedly presented stimulus. Habituation is a decremental process that is assumed to occur within the S-R pathway, while sensitization is an incremental process that effects the organism's state, increasing the tendency to respond. The two processes of habituation and sensitization are assumed to occur concurrently in conditions of repetitive presentation of an effective stimulus, and they interact to produce the net behavioural output.

There are twelve assumptions contained in this theory:

1. The development of habituation proceeds in an exponential manner and reaches an asymptotic level.
2. Habituation decays spontaneously when stimulation is stopped.
3. The rate and degree of habituation is directly related to the frequency of the repeated stimulation, and is inversely related to the intensity of the eliciting stimulus.
4. A repeated series of repetitive stimulation results in progressively more habituation.
5. There is some degree of generalization of habituation to a test stimulus.
6. Sensitization occurs in state systems but not in S-R pathways.
7. During a series of repetitive stimulus presentation sensitization first grows, then decays.
8. Amount and duration of sensitization are directly related to both frequency and intensity of the eliciting stimulus.
9. Sensitization decays spontaneously when stimulation stops.
10. Sensitization exhibits generalization.
11. Dishabituation is an instance of sensitization.
12. Temporal conditioning of sensitization can occur under some conditions.

B. Two-factor dual-process theory:

Petrinovich (1984) has proposed a more updated version of the dual-process theory that includes two new factors: stimulus specificity and relative permanence. Stimulus specificity refers to the extent to which changes in response are the product of the explicit eliciting stimulus (stimulus specific), or are due to repeated exposure to the environmental context in which this stimulation occurs (stimulus general). Relative permanence was included to account for changes in response magnitude that occur within a series of repeated stimulation (short-term) and those that occur over several series of such stimulation (long-term). Relative permanence and stimulus specificity vary along continuous scales, as do the observed effects of response habituation and sensitization, and where along these scales they lie depends on exact nature ofthe response preparation.

C. Parametric features of a sensitization based model of SIP:

There are a number of things that a model of SIP based on current theories of response habituation must achieve. First, the response in question, namely drinking, must conform to the parametric features described in these theories. For example, drinking should be a function mainly of the frequency and intensity of stimulus presentation (Groves and Thompson, 1970). Second, if it is assumed that excessive drinking is a manifestation of sensitized

behaviour, then it should be possible to demonstrate instances of habituation of this same behaviour, under appropriate conditions. Third, the immense body of data on SIP must be consistent with any proposed descriptive model.

Progressive development of SIP.

Wetherington (1982) has pointed out the most basic similarity between SIP and other sensitized behaviour: There is a progressive increase in measures of response magnitude over time with exposure to an intermittently and repeatedly presented stimulus. In the proposed model of SIP as a sensitized behaviour, this progressive development over sessions is taken to reflect long-term sensitization as described by Petrinovich (1984). The two-factor dual-process theory predicts that sensitization will decay over time after stimulation is stopped. There is no specific decay time for sensitization as this depends on the nature of the preparation being examined. Substantial decay may not be evident until several weeks later as in the case of stimulant induced behavioural sensitization (Robinson and Becker, 1986), or it may occur within minutes. SIP decay time appears to be relatively long, with substantial decrements in volume drunk in a 1 hour FT60 schedule with 45mg pellets occurring somewhere between 10 weeks and 6 months after initial training to asymptote (Wetherington and Riley, 1986).

Frequency and intensity of food reward.

Dual-process theory states that in situations of high stimulus intensity response facilitation will predominate, and this will be the case even more so when stimulus frequency is moderate to low (Groves and Thompson, 1970). Conversely, response decrements will prevail when the repeated stimulus is one of low intensity, and when frequency of stimulus presentation is high. Dealing with stimulus frequency first, with intensity held constant, the bitonic function relating interfood-interval to SIP levels should be recalled. Increasing interval length is equivalent to decreasing stimulus frequency (i.e., food delivery). Between interval lengths of 4-seconds to 120-seconds, the rate of water intake increases as interval length increases (Falk, 1966). This would be predicted by dual-process theory when stimulus intensity is constant, as it is in the common SIP experiment with standard 45mg pellets. The decreasing part of the bitonic function relating stimulus frequency to drinking levels is also predicted by dual-process theory. When frequency is too low there will be little sensitization, and therefore, one would expect that decreasing stimulus frequency (i.e., increasing interfood interval length) would cause response increments only up to a point after which the incremental processes would decline with further frequency reductions (Flory,1971; Wayner and Greenberg, 1973). Thus, the bitonic function relating interfood interval length to volume consumed is predicted by

the sensitization model of SIP.

It is assumed that a relevant dimension along which intensity of a food stimulus can be measured is the texture gradient, but another dimension that would likely be as valid could be the amount of food delivered. The appeal of these assumptions is bolstered in light of recent demonstrations by Miller (1981) of the necessity of oral somatosensation for the initiation and control of ingestive behaviour. Miller deafferented rats to produce various degrees of oral somatosensory impairment and found that the greater this impairment, the less investigative activity, eating bouts, and water spout exploration a rat was likely to partake in; the amount of ingestive behaviour was directly related to the amount of orosomatic stimulation the animal was capable of receiving.

In the present study stimulus frequency was held constant at one presentation per minute, but the intensity of the stimulus was varied by manipulating the texture of the food. When the intensity of the food stimulus was high (i.e., pellets or coarse granular), the amount of drinking was likewise high. When the intensity of the food stimulus was low (i.e., finer granular), the drinking levels were likewise low. Furthermore, not only was less sensitization of drinking evident in the animals that recieved 'low-intensity' food as revealed by their lower levels of drinking relative to those rats recieving 'high-intensity' food, but in the former animals there was also evidence of

habituation of the drinking response within the session, and the rate of habituation appeared to increase with decreases in stimulus intensity. All of the foregoing results would be predicted by dual-process theory, if food texture were a relevant stimulus intensity dimension for drink elicited behaviour.

Although discrepancies exist within the literature, the majority of the evidence suggests that the relationship between size of food reward and SIP is an inverse one (Reid and Staddon, 1982; 1987). At first glance, this might appear to mitigate against SIP as a sensitized behaviour because, intuitively, more food should be a more intense stimulus. Studies showing an inverse relationship between meal size and drinking on intermittent schedules have manipulated the number of 45mg food pellets delivered per interval. When a rat is faced with the delivery of several pellets rather than one, he consumes these, one at a time, in rapid order. Since the pellets are eaten one at a time, the intensity of the oral tactile stimulation should not differ from that produced by a single pellet delivery; only the *duration* of this stimulation should be greater. Increasing the duration of a repeatedly presented stimulus has the effect of increasing the rate habituation to that stimulus (Wickelgren, 1967).

If tactile stimulation of the oral cavity is a factor mediating the sensitization of food elicited drinking, then increasing the duration of each stimulus presentation while

keeping intensity constant, would be expected to attenuate the amount of sensitization and increase the rate of habituation. Reid and Staddon (1982), in addition to finding that less drinking occurred in sessions as reward size (number of pellets) increased, also found that increasing reward size increased the rate of decline in lick rate within a session, consistent with the prediction of increased rate of habituation with increased stimulus duration. It should be recalled, also, that decreasing food granulation size in the present study led to less and less drinking, while time spent in oral and perioral contact with food and/or the feeder mechanism increased, and that when session totals are considered, this suggests an inverse relationship between the duration of tactile stimulation, and subsequent drinking. This latter effect might be enough to account for the observed decrements in drinking over the session, without assuming that the texture of the food legitimately determines its intensity as a drink eliciting stimulus.

Body weight and food deprivation.

The fact that SIP is greatly dependent on food deprivation level of the organism is quite congruent with the proposed model. Recall that the dual-process theory postulates that habituation occurs within the S-R pathway and that sensitization occurs through influences on the "state" of the organism. By "state" is meant the activation,

arousal, or tendency to respond of the organism (Groves and Thompson, 1970). Furthermore, any means by which the "state" systems of the organism are positively activated should have the effect of interfering with response habituation. This could be viewed as an enhanced propensity for sensitization. Food deprived rats are known to be highly aroused relative to satiated rats (Brett and Levine, 1979, 1980; Tazi, Danzer, Mormede, and Le Moal, 1986) and would therefore be expected to have a high level of state activation on which the superimposition of sensitizing stimulus should have a further response facilitating effect (Wetherington, 1982). In satiated rats there is little state activation prior to the onset of an experimental session of intermittent food delivery, and therefore, the habituation process is allowed to reveal itself early, thus preventing the amount of drinking to become excessive. In Groves and Thompson's words, "the extent to which sensitization habituates below control level may also depend in part on the initial base-line state of the organism ...", (p. 441). In the case of food deprived rats recieving pellets intermittently, the hypothesized sensitization does not habituate noticeably within the typical session, possibly because the initial baseline level of state activation of the animal is very high.

Summary.

Evidence has been presented that suggests that the results of the present study can be interpreted as supporting the view of SIP as a sensitized behaviour, based on current theories of sensitization and habituation. In addition to the basic similarities between SIP and sensitized behaviour that are reflected in the progressive development of both over time with repeated presentation of a stimulus, and decay over time, data from other SIP studies which examined the effects of certain of the parameters that are most potent in influencing the development of SIP have also been shown to be interpretable in terms of sensitization theory. Among the factors that have been found to produce effects on SIP and that are congruent with the proposed model are 1) interfood interval length, 2) size of food reward, 3) degree of food deprivation.

VII. FIGURES

FIGURE CAPTIONS

Figure 1. Group means for volume drunk in ml on each session. Vertical lines join nonsignificantly different group means, Duncan Multiple Range, $p<0.05$. Standard errors for Groups PEL to 0.2 were, respectively, 2.42, 1.35, 1.33, 1.62, 1.69, 1.06, 0.69.

Figure 2. Mean percent of total session time engaged in each behaviour for each group. Asterisks denote significant differences from pellet control group (PEL). * = $p<.05$, ** = $p<.01$.

Figure 3. Mean bout frequency per session (top graph) and mean transformed bout duration (bottom graph) for drinking for each group. Asterisks denote significant differences from pellet control group (Group PEL). * = $p<.05$, ** = $p<.01$, . The transformation performed on bout duration was the square root of the absolute drinking bout duration in seconds, plus 1.

Figure 4. Percent-time for drinking, rearing, and feeder-poke, across trials within Session 15. Vertical bars connect nonsignificantly different group means (Duncan's Multiple Range, $p<0.05$). Asterisks denote significant differences from value on Trial 1; (Duncan's Multiple Range $p<0.05$). Standard errors for all groups on PT drink were between 0.90 - 3.41, on PT rear 0.80 - 3.06, and on PT feeder-poke 1.83 - 5.04.

Figure 5. Mean bout frequency for drink and rear, across trials on Session 15. Vertical bars connect nonsignificantly different group means (Duncan's Multiple Range, $p<0.05$). Asterisks denote significant differences from value on Trial 1; Duncan's Multiple Range, $p<0.05$. Standard errors for all groups on BF drink were between 0.008 - 1.11, and on BF rear between 1.05 - 3.19.

Figure 6. Mean transformed bout duration for drink and rear, across trials on Session 15. Vertical lines connect nonsignificantly different group means (Duncan's Multiple Range, $p<0.05$). Asterisks denote significant differences from value on Trial 1; Duncan's Multiple Range, $p<0.05$. Standard errors for all groups were between 0.15 - 0.27 for BD drink, and between 0.06 - 0.10 for BD rear.

Figure 7. Temporal distribution of the different behaviours within the interfood-interval for each group, averaged over all coded intervals within Session 15, for drink, feeder-poke, rear, investigate, groom, and locomote. The ordinate scale is the mean percent time within a 6-second bin spent engaged in the behaviour. The abcsissa marks each of the ten 6-second bins within the FT60 second interval. Group PEL=filled circles, Group 1.2=open triangles, Group 1.0=open squares Group 0.8=filled triangles, Group 0.6=open circles, Group 0.4=inverted triangles, Group 0.2=filled squares. Vertical lines completely transect lines representing nonsignificantly different group means in each bin, Duncan's Multiple Range, $p<0.05$. Standard errors for all groups on drink were between, 0.92 - 3.41, on feeder-poke, 2.26 - 7.12, on rear 0.79 - 3.05, on groom 0.55 - 3.42, on investigate 1.57 - 3.99, and on locomote 0.33 - 0.64.

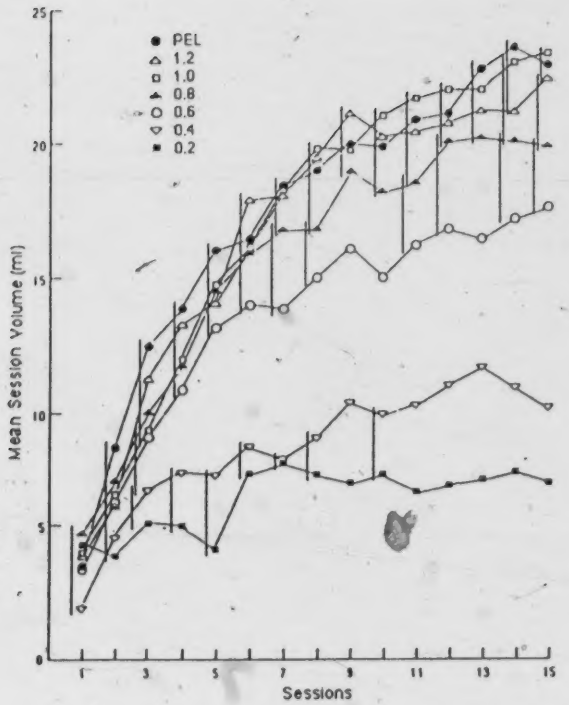

FIGURE 1

Group means for volume drunk on each session.

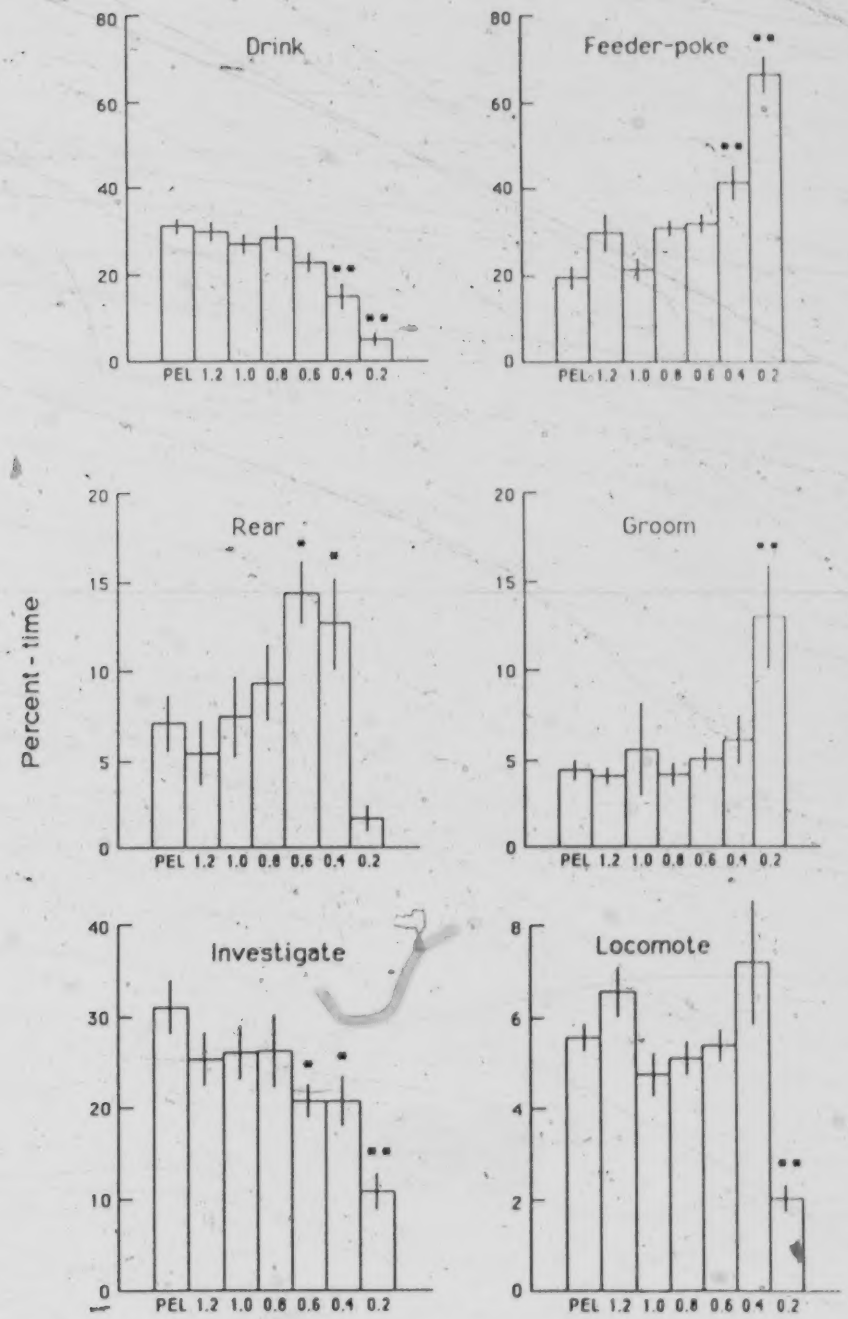

FIGURE 2

Mean percent-time spent in each behaviour.

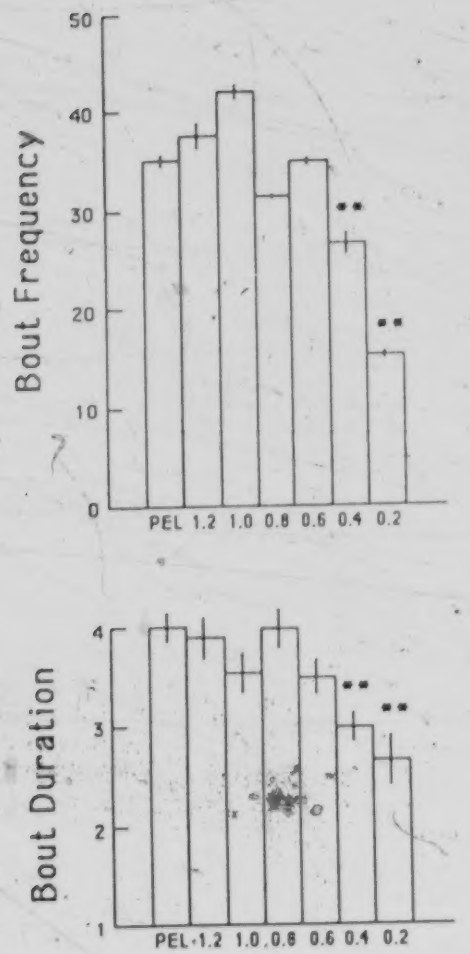

FIGURE 3

Mean bout frequency and bout duration of drinking.

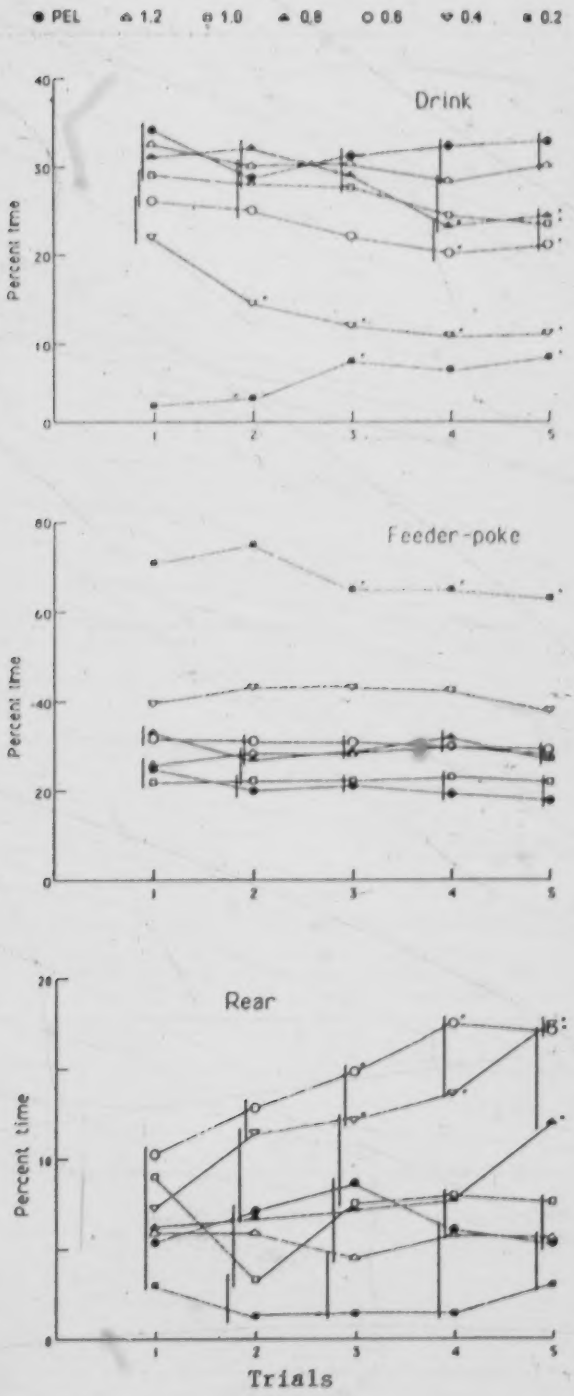

FIGURE 4

Percent-time for drinking, feeder-poke, and rearing.

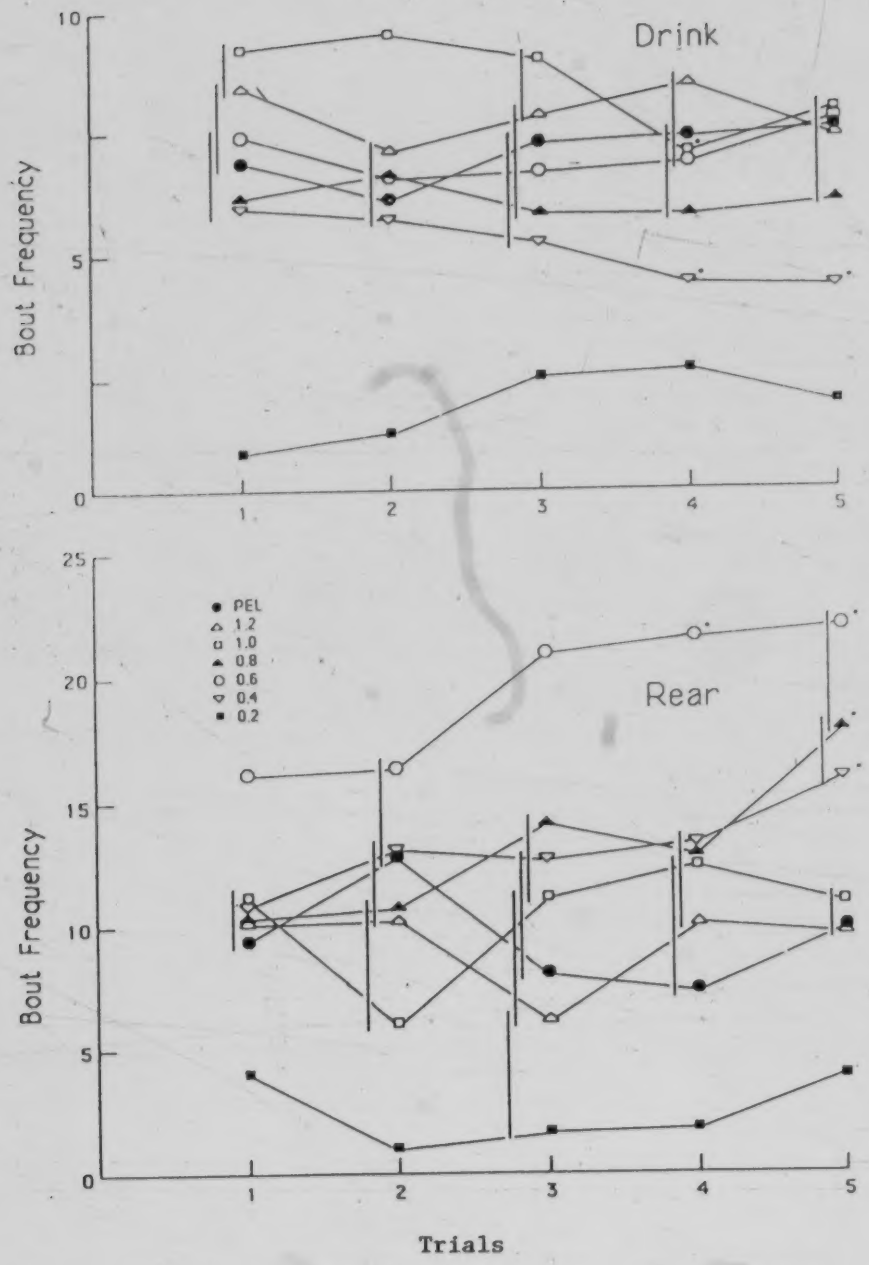

FIGURE 5

Mean bout frequency for drink and rear, across trials on Session 15.

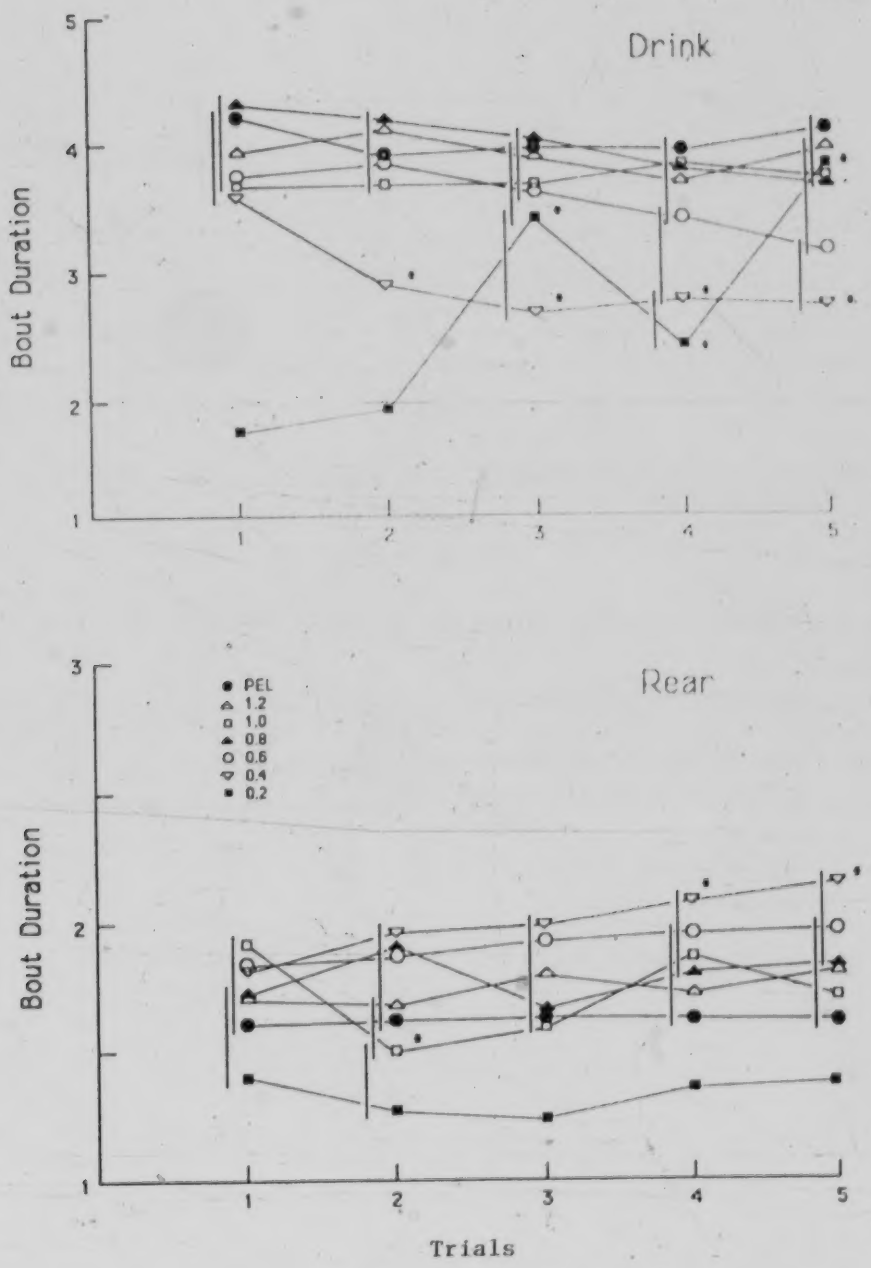

FIGURE 6

Mean transformed bout duration for drink and rear, across trials on Session 15.

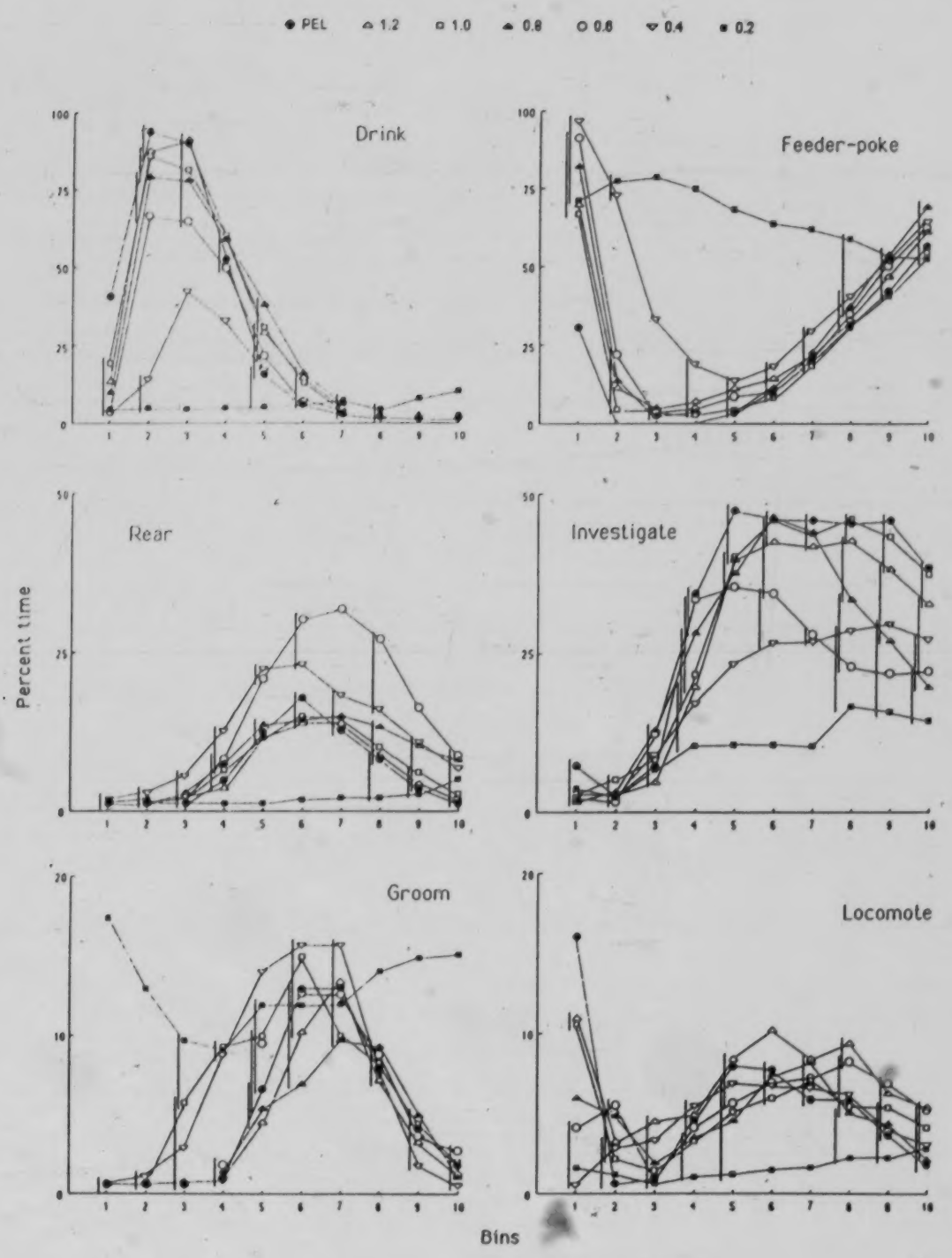

FIGURE 7

Temporal distribution of behaviours within the interfood interval.

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